Universitat d'Alacant
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The role of marine offshore protected areas in protecting large pelagics. Practical case: Cocos Island National Park. (Costa Rica)

El papel de las áreas marinas protegidas en alta mar en la protección de grandes pelágicos. Caso práctico: Parque Nacional Isla del Coco. (Costa Rica)

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DOCTORADO EN CIENCIAS DEL MAR Y BIOLOGIA APLICADA

Dirigida por:
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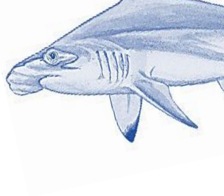

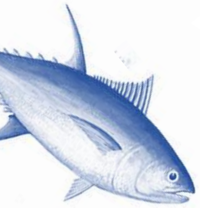

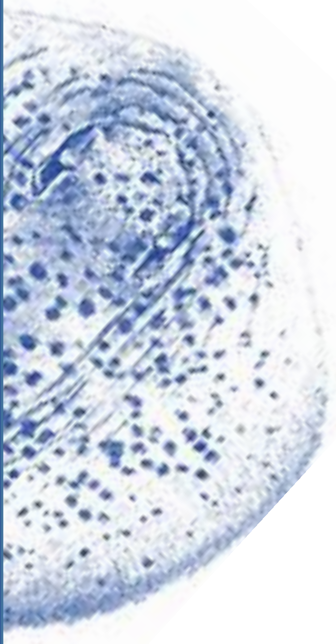

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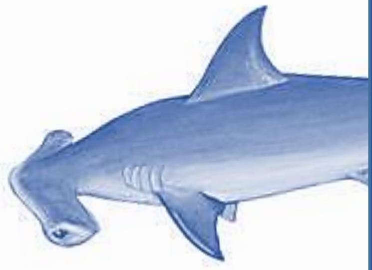

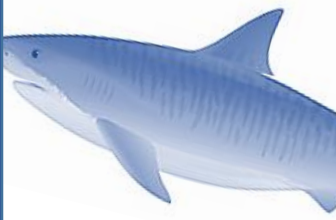

TABLE OF CONTENTS

LIST OF ARTICLES

Chapter 2. Gonzáles-Andrés, C., FM Lopes, P., Cortés, J., Sánchez-Lizaso, J. L., & Pennino, M. G. (2016). Abundance and distribution patterns of *Thunnus albacares* in Isla del Coco National Park through predictive habitat suitability models. Plos one, 11(12), e0168212.

Chapter 3. Predictive habitat suitability models to aid the conservation of elasmobranchs in the Isla del Coco National Park (Costa Rica). Submitted in Marine Biology.

Chapter 4. González-Andrés, C., Sánchez-Lizaso, J. L., Cortés, J., & Pennino, M. G. (2020). Illegal fishing in Isla del Coco National Park: Spatial-temporal distribution and the economic trade-offs. Marine Policy, 119, 104023.

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> “Necesito del mar porque me enseña:
> no sé si aprendo música o conciencia:
> no sé si es ola sola o ser profundo
> o sólo ronca voz o deslumbrante
> suposición de peces y navíos.
> El hecho es que hasta cuando estoy dormido
> de algún modo magnético circulo
> en la universidad del oleaje...”
> Pablo Neruda

LIST OF FIGURES

Chapter 2

Chapter 3

Chapter 4

Fig. 1. Map of Isla del Coco National Park. (http://www.mpatlas.org/mpa/).

Fig. 2. Smooth functions for the selected covariates of the illegal fishing model. The solid line in each plot is the estimated smooth function, and the dashed lines represent approximate 95% confidence intervals.

Fig. 3. Spatial distribution maps of illegal fishing operations in PNIC aggregated at quarterly intervals: January-March; b) April-June; c) July-September; d) October-December.

Fig. 4. The spatial patterns of the yellowfin tuna abundance (n. of individuals) in PNIC aggregated in at quarterly intervals: a) January-March; b) April-June; c) July-September; d) October-December.

Fig. 5. The spatial patterns of the silky shark abundance (n. of individuals) in PNIC aggregated in at quarterly intervals: a) January-March; b) April-June; c) July-September; d) October-December.

Fig. 6. Spatial distribution maps of the benefits ($USD) of illegal fishing in PNIC aggregated at quarterly intervals: a) January-March; b) April-June; c) July-September; d) October-December.

Fig.7. Spatial distribution maps of the costs ($USD) of illegal fishing in PNIC aggregated at quarterly intervals: a) January-March; b) April-June; c) July-September; d) October-December.

Fig. 8. Spatial distribution maps of the profits ($USD) of illegal fishing in PNIC aggregated at quarterly intervals: a) January-March; b) April-June; c) July-September; d) October-December.

Fig. A1. Supplementary Material. The spatial patterns of the environmental variables considered to be potential predictors of illegal fishing in the Isla del Coco National Park.

Fig. A2. Supplementary Material. Pearson's correlation matrix of explicative variables used in models.

LIST OF TABLES

Chapter 2

Chapter 3

evaluated by AUC: area under the receiver-operating curve, SENS: model sensitivity; SPEC: model specificity and TSS: True Skill Statistic.

Table S1 Supplementary Material**:** Predictores variables used fro modeling the elasmobranch occurrence in the Isla del Coco. SST = Sea Surface Temperature, SSS = Sea Surface Salinity, Chl-a = Chlorophyll-a.

Table S2 Supplementary Material: Correlation matrix of the environmental variables included in the model.

Chapter 4

Table 1. Numerical summary of the dataset. The variables are: the year in which the illegal fishing was recorded (2004-2009); the quarter- January-March (1), April-June (2), July-September (3) and October-December (4); the number of confiscated longlines; the number of yellowfin tuna and the number of sharks.

Table 2. Comparison of the most relevant GAM models performed to understand the illegal fishing abundance and distribution. Selection of the model was based on the scores of the Akaike information criterion (AIC), the Un-biased Risk Estimator (UBRE) and the total percentage of deviance explained by each model (% DE). Variable acronyms are: bathymetry (B), distance from the coast (D), slope (S), rugosity (R); Quarter (Q), abundance of the shark (SH), and abundance of yellowfin tuna (T). The best model is highlighted in bold. The significance of the predictors is indicated by *.

Resumen

Estado de la pesca mundial: grandes pelágicos y elasmobranquios de arrecife

Los recursos pesqueros han mostrado un deterioro gradual y constante en las últimas décadas [1-5]. Según la FAO (SOFIA 2018), la parte de las poblaciones de peces que se encuentran dentro de niveles biológicamente sostenibles ha mostrado una tendencia a la baja del 90% en 1974 al 66,9% en 2015 y el porcentaje de poblaciones explotadas a niveles biológicamente insostenibles se incrementó del 10% en 1974 al 33,1% en 2015. La sobreexplotación pesquera también ha afectado a las grandes pesquerías de depredadores pelágicos (tiburones, atunes y marlines) en todo el mundo [6-10]. Este efecto global ha llegado incluso a las partes más remotas del océano como los conocidos "santuarios" [6].

La mayoría de las artes de pesca utilizadas hoy en día son poco selectivas efectuándose la captura incidental de especies que en un principio no son especies objetivo de la actividad pesquera (captura no deseada). La captura incidental es un factor que afecta la biodiversidad marina y está asociada a artes de pesca poco selectivos que capturan millones de toneladas de organismos vertebrados e invertebrados que posteriormente son desechados en el mar [11]. Adicionalmente muchos de los artes de pesca usados en la actualidad degradan y destruyen los habitas marinos más importantes, como los fondos oceánicos. Unos de los grupos sometidos a mayor presión por la actividad pesquera son los grandes depredadores como los tiburones y las rayas [6].

Los tiburones y las rayas se consideraban la captura incidental menos valorada frente a las poblaciones de pesca más rentables, como el atún (Scombridae) y el bacalao (Gadidae). Sin embargo, la creciente demanda de productos, junto con la disminución de pesquerías valiosas, dio como resultado un aumento de las capturas y la retención de tiburones y rayas [12]. Hasta hace poco, las pesquerías dirigidas e incidental de tiburones y rayas estaban sometidas a poca gestión y fueron de escasa prioridad en la gestión pesquera [13].

La preocupación por la sostenibilidad de las pesquerías de tiburones y rayas impulsó avances en las herramientas de gestión de las pesquerías de elasmobranquios durante los últimos veinte años. En un principio, en 1999, la Organización de las Naciones Unidas para la Agricultura y la Alimentación (FAO) recomendó el desarrollo y la implementación de Planes Nacionales de Acción para los tiburones. Estos planes no vinculantes tenían diez objetivos que abarcaban; la sostenibilidad, las especies amenazadas, la consulta a las partes interesadas, la minimización de desechos, las consideraciones del ecosistema, la mejora del seguimiento y la presentación de informes de capturas, desembarques y comercio. En los últimos 20 años han incluido: (a) la introducción de prohibiciones de comercio de aletas [14]; (b) aplicación de las regulaciones comerciales de peces marinos a través de la Convención sobre el Comercio Internacional de Especies Amenazadas (CITES) [15]; (c) acuerdos internacionales para prevenir la pesca ilegal, no reglamentada y no declarada [16]; y (d) gestión y conservación de tiburones y rayas migratorias a través del Memorando de la Convención sobre especies migratorias para tiburones [17].

A pesar de los avances en la ordenación de las pesquerías de elasmobranquios, existe la preocupación de que las pesquerías de condrictios siguieran el patrón predecible basado en la disminución de la captura por unidad de esfuerzo, colapso y agotamiento en serie [18]. De hecho, los desembarques de tiburones y rayas aumentaron un 227% desde 1950 (el primer año de recopilación de datos) hasta el año 2003 donde se apreció un pico en las capturas y, posteriormente, disminuyeron casi un 20% hasta 2011 (FAO 2013).

En un principio, esta reducción en los desembarques de tiburones y rayas se esperaba que fuera debido a un aumento de las pesquerías sostenibles y, por lo tanto, a la reducción de las capturas ya que las especies objetivo serian otras diferentes a los elasmobranquios. Otra posibilidad era que reducción en los desembarques de tiburones y rayas fuera debido a la disminución de su población (FAO, 2010). Sin embargo, años después, se estimó la posibilidad de interpretar los datos de forma más compleja con la siguiente idea; “no es posible una explicación simple de las tendencias (de los desembarques) recientes” (FAO 2014).

Davidson, et al. (2016) [19] prueba la hipótesis de la FAO y evalúa si la variación en los desembarques de tiburones y rayas entre 2003 y 2011 se explicaba mejor mediante indicadores de sobrepesca o de la aplicación de la ordenación pesquera. Señalan que la mejora reciente en la ordenación pesquera nacional o internacional aún no era lo suficientemente fuerte como para explicar la reciente disminución de los desembarques de condrictios, así pues, las disminuciones de los desembarques se relacionaron más estrechamente con la presión pesquera.

Los grandes depredadores como los elasmobranquios y tunidos desempeñan un papel fundamental en el ecosistema marino [20] manteniendo ecosistemas complejos, proporcionando fuentes de alimento para los carroñeros [21] y regulando el tamaño y la dinámica de las poblaciones de presas eliminando a los individuos débiles [22,23]. La eliminación selectiva de depredadores puede dar lugar a cambios en las interacciones tróficas [4,24,25] que se verán reflejados a nivel comunitario.

Algunas especies depredadoras son especialmente sensibles a la sobreexplotación, en particular los elasmobranquios, que por sus características biológicas (longevidad, poca progenie y maduración sexual tardía) no pueden soportar una alta mortalidad prolongada en el tiempo [26-28].

Actualmente se estima que las grandes poblaciones de depredadores han disminuido en un 90% durante los últimos 50 años, debido a la explotación industrial [6.29]. Según la Convención de las Naciones Unidas sobre Poblaciones de Peces Altamente Migratorias, mayo de 2006 [30] la pesca mundial con palangre en alta mar debe reducirse significativamente para revertir el proceso de agotamiento de las poblaciones de atunes, tiburones y otras poblaciones de peces. Si el declive continúa, la extinción de poblaciones y especies sensibles es una amenaza real. Diferentes estudios han confirmado la desaparición de los elasmobranquios. Aldebert, (1998) [31] indica la desaparición de 14 especies de elasmobranquios del Golfo de León (Mediterráneo noroccidental) y según Quero (1998) [32], nueve especies de elasmobranquios han desaparecido del Cantábrico entre 1957 y 1995.

En concreto, la sobrepesca de atún de aleta amarilla y tiburones se ve favorecida por el alto valor económico en los mercados nacionales e internacionales [33,34] tanto por su carne como por sus subproductos: aceite de hígado de tiburón, piel y aletas [35,36].

Así pues, podemos señalar que la sobrepesca, junto con otros factores de origen antropogénicos, como la degradación del hábitat y los cambios en los sistemas marinos, alteran directamente la composición de las comunidades ecológicas y la estructura y productividad de los sistemas marinos [37].

Situación de la pesquería pelágica en Costa Rica

Los recursos marinos costeros de Costa Rica han estado sometidos a una fuerte presión económica y ambiental durante décadas. El Golfo de Nicoya es reconocido ampliamente como el sistema marino más productivo del país, se encuentra severamente sobreexplotado. En términos generales, se observa que los niveles de producción pesquera se han mantenido como consecuencia del aumento de la captura de especies pelágicas no tradicionales, como el tiburón, la llampuga (*Coryphaena hippurus*) [38-40]. Además, el esfuerzo pesquero (número de embarcaciones, número de horas en el mar) ha aumentado y se observa una reducción de los recursos tradicionales, como corvina (*Pseudosciaena crocea*), róbalo (*Centropomus undecimalis*), pargo (*Pagrus auratus*) y congrio (*Conger sp*) [41,42].

La pesca de palangre o “longline” es una pesquería multiespecífica que impacta a diferentes especies en diferente medida, dependiendo del esfuerzo pesquero y sus propias características biológicas [43]. El impacto en los grandes pelágicos como los elasmobranquios ha ido en aumento a lo lardo de las últimas décadas. Los grandes pelágicos han excedido su rendimiento máximo sostenible, mostrando reducciones del 22% en los recursos pelágicos desembarcados en el país [44]. Específicamente, la captura de elasmobranquios muestra signos de agotamiento con disminuciones del 60% en su abundancia relativa entre 1991 y 2001 [45,46].

El atún aleta amarilla (*Thunnus albacares*) y el atún patudo (*Thunnus obesus),* recursos clave para la industria nacional, también se encuentran en problemas debido a la sobrepesca, mostrando un grave deterioro en el estado de sus poblaciones [45,47]. Según la Comisión Interamericana del Atún Tropical (2004) [47], los atunes capturados actualmente son muy pequeños, muy por debajo del tamaño recomendado para una producción máxima sostenible.

En términos generales, la sobreexplotación de depredadores pelágicos radica en un uso desordenado de la actividad pesquera que compromete la sostenibilidad de las actividades económicas y las condiciones de vida de las poblaciones humanas que directa o indirectamente dependen de estos recursos y que afectan al patrimonio de biodiversidad del país.

Áreas marinas protegidas oceánicas

Las Áreas marinas protegidas (AMPs) también se les conoce como reservas marinas, reservas naturales marinas, santuarios marinos o áreas especialmente protegidas. Según la definición dada en 1994 por la Unión Mundial para la Conservación (IUCN), un AMP es «un área de mar especialmente destinada a la protección y mantenimiento de la diversidad biológica y de los recursos naturales y culturales asociados y gestionada por ley u otros medios efectivos de control». Ésta es una definición muy amplia e incluye una gran variedad de posibles significados, dependiendo de cuál sea el principal objeto de conservación (patrimonio natural, patrimonio cultural o producción sostenible), el nivel de protección que se pretende conseguir (sin acceso, sin impacto, sin explotación de recursos, delimitación de las zonas de explotación de recursos o delimitación de diferentes usos por zonas), la duración de la protección (permanente, condicional o transitoria), la constancia de la protección (anual, estacional o rotatoria), la escala ecológica de la protección (a nivel de ecosistema o de un recurso específico) y las restricciones de la explotación (sin restricciones, explotación con regulación, explotación exclusivamente para pesca comercial, explotación exclusivamente para pesca recreativa, pesca sin muerte, explotación para pesca de subsistencia o explotación por motivos científicos o educativos) (NMPAC, 2005) [48].

La creación de las AMPs son una herramienta esencial para la conservación y restauración de las especies marinas. Las AMPs proveen refugio para que las poblaciones de peces que han sufrido sobre explotación se recuperen, y que los hábitats modificados por la pesca se regeneren [49]. Mientras existan controles eficientes, es de esperar que las condiciones de pesca en zonas aledañas también mejoren, por la mayor exportación de larvas (subsidio de reclutamiento) y la migración de adultos [50].

Si bien la mayoría de las discusiones sobre las AMP se han centrado en los hábitats cercanos a la costa, como las comunidades intermareales y arrecifes de coral, las áreas protegidas rara vez se han considerado en la conservación de especies pelágicas [51].

Las AMPs no se habían visto como una herramienta de protección y conservación de especies pelágicas debido a la naturaleza abierta y dinámica de alta mar, que dificulta el diseño y la aplicación de las AMPs [52]. Tradicionalmente, los sistemas pelágicos se gestionan con enfoques de una sola especie, la conservación se basa en la mejora de las regulaciones (por ejemplo, aplicación de cuotas y restricciones de tamaño) y la modificación de los artes de pesca. Muchas de estas regulaciones dependen del conocimiento científico exacto de la ecología de la especie como los patrones migratorios, preferencias de hábitat y variabilidad de la dinámica poblacional. Esta información es difícil de obtener y no suele estar disponible para especies sin importancia comercial como, por ejemplo, captura incidental [53].

Los diseños de reservas deben relacionarse con la ecología (por ejemplo, hábitats, ámbitos y migraciones), biología de la especie (tipo de reproducción, alimento) y la variabilidad inherente de sus hábitats (por ejemplo, perturbaciones, regímenes oceanográficos y cambio climático) [54]. La distribución de las especies pelágicas está determinada en gran medida por las complejidades del flujo de agua, y por el acoplamiento de procesos físicos y biológicos que promueven el crecimiento y retención de poblaciones planctónicas [55,56]. Estos, a su vez, son mediada a grandes escalas de tiempo y espacio, entre estaciones y décadas y de decenas a miles de kilómetros [57].

Así pues, en los sistemas pelágicos, donde muchas especies se distribuyen miles de millas, y donde las rutas migratorias son dinámicas y poco entendidas, la conservación de especies altamente móviles y migratorias sigue siendo un desafío muy serio. Las AMP deberán guiarse por una comprensión de la biología de la especie y hábitat de preferencia.

Características generales de las islas oceánicas y los montes submarinos

Las islas oceánicas y los montes submarinos pueden crear condiciones tales como un aumento de los flujos de nutrientes verticales y la retención de material que promueven la productividad alimentando diferentes niveles tróficos [58-60] como los depredadores pelágicos (tiburones y atunes) [60,62]. Además, estas áreas también proporcionan paradas de descanso y estaciones de limpieza [63]. Estas combinaciones de factores hacen que los montes submarinos y las islas oceánicas sean lugares adecuados de apareamiento, alimentación y cría de especies pelágicas altamente migratorias, así como de organismos bentónicos [64].

En general, los montes submarinos ubicados en aguas poco profundas e islas oceánicas son áreas de alta ocurrencia de la biota pelágica [63,65-69] siendo puntos críticos de alta biodiversidad. Estas asociaciones de especies pelágicas con montes submarinos se han descrito previamente para algunas especies de atunes [63,70,71], tiburones [69,72] y peces picudos [72,73]. Por tanto, los montes submarinos y las islas oceánicas son puntos críticos para la biodiversidad pelágica y pueden ser áreas adecuadas para la conservación de los ecosistemas oceánicos [75].

Áreas marinas protegidas aplicadas a la protección de grandes pelágicos.

Para las AMPs aplicadas a la protección de grandes pelágicos podemos señalar como ejemplo las AMPs existentes para tiburones. Estas AMPs se pueden clasificar en 3 categorías: a) AMPs virtuales o reales, donde la legislación gubernamental ha designado ciertas especies como protegidas en aguas dentro de su jurisdicción; b) AMPs oficiales para tiburones, que son áreas designadas específicamente para la protección de especies de tiburones y que generalmente están orientadas hacia objetivos ecológicos; y c) las AMPs de prohibición de captura destinadas a ser una herramienta de ordenación pesquera para los tiburones. Las AMPs más comunes son las del primer tipo, las AMPs virtuales [76].

Actualmente, hay al menos cinco especies de elasmobranquios protegidos a través de legislación especial en todo el mundo debido a su vulnerabilidad a la sobreexplotación. Algunos ejemplos son el tiburón blanco (*Carcharodon carcharias*) es la especie de tiburón más protegida en todo el mundo; el tiburón ballena (*Rhincodon typus*), está protegido en Florida y todas las aguas federales de las costas estadounidenses del Golfo de México y Atlántico Occidental, en Maldivas y en Australia Occidental; el tiburón peregrino (*Cetorhinus maximus*) está protegido en las aguas de Florida, todas las aguas federales de los Estados Unidos, las costas del Golfo de México y el Océano Atlántico, la Isla del Hombre, el Mar Mediterráneo y Nueva Zelanda; el tiburón tigre (*Odontaspis noronhai*) en las riberas federales de las costas estadounidenses del Golfo de México y el Océano Atlántico. Otros elasmobranquios protegidos en Florida son el tiburón sierra (*Pristiophorus schroederi*), la raya águila (*Aleobatus narinari*) y el pez sierra (*Pristis* spp). Finalmente, el Convenio de Barcelona incluye la protección de varias especies en el Mediterráneo como el tiburón peregrino (*Cetorhinus maximus*) y la raya diablo gigante (*Mobula mobular*), considerados en peligro o amenazados [77].

En el caso de AMPs focalizadas en elasmobranquios, hay que tener en cuenta que la diversidad de especies de tiburones [77]; incluye una gran variedad de tamaños, biología y hábitats que presentan un gran desafío para el diseño de AMP para su protección. La dinámica de la población también varía enormemente entre los tiburones. La longevidad puede ser relativamente alta o baja dependiendo de la especie, por ejemplo, la musola pintada (*Mustelus canis*) alcanza la madurez sexual a los dos años, mientras que el tiburón arenero (*Carcharhinus obscurus)* la alcanza a los 20 años. También hay grandes diferencias en el número de progenie. El rango de fecundidad oscila entre siete alevines por camada en el tiburón nariz afilada, 40-80 en el tiburón tigre (*Galeocerdo cuvier*) y alrededor de 300 en el tiburón ballena [76].

Los ecosistemas pelágicos no solo se enfrentan a las amenazas de la sobrepesca, sino que también hay que sumar factores como la contaminación, el cambio climático, la acidificación de los océanos, el transporte marítimo, la eutrofización y la introducción de especies [78]. La protección de los ecosistemas pelágicos será fundamental para alcanzar los objetivos mundiales de conservación marina, como el llamado del Convenio sobre la Diversidad Biológica (CDB) de proteger el 10% de los océanos del mundo a través de áreas marinas protegidas (AMPs) para 2020 (Convenio sobre la Diversidad Biológica 2010) [79].

En las últimas décadas se ha desarrollado la idea de que los ecosistemas de mar abierto pueden protegerse identificando puntos críticos de biodiversidad [6,75] como ubicaciones potenciales para reservas marinas en alta mar [20,80]. Las áreas marinas protegidas pelágicas (AMPPs) pueden ser lo suficientemente grandes para protegerse contra amenazas e incorporar partes clave de hábitats y movimientos de animales de gran alcance o migratorios. [81-83].

Es importante mencionar que el dinamismo de los ambientes pelágicos puede reducir significativamente la efectividad de las medidas de conservación [84]. Por lo tanto, es necesario crear una red de Áreas Marinas Protegidas (AMP), o áreas cerradas temporal y espacialmente, en áreas de cría, migración y reproducción de especies sensibles o explotadas comercialmente. Esta red de AMP es esencial para proteger la biodiversidad pelágica y lograr la sostenibilidad de las especies de depredadores marinos [84]. Podemos señalar como ejemplo de tal iniciativa "El Corredor Biológico del Pacífico Oriental" suscrito en abril de 2004, en San José (Costa Rica) por los gobiernos de Colombia, Ecuador, Costa Rica y Panamá, Este “corredor” está formado por las Islas Oceánicas de Galápagos (Ecuador), Cocos (Costa Rica), Coiba (Panamá), Malpelo y Gorgona (Colombia).

Game et al. (2009) [81] argumentan que “los avances recientes en la ciencia de la conservación, la oceanografía y la pesca proporcionan la evidencia, las herramientas y la información para ... confirmar que las AMPPs son instrumentos defendibles y factibles para la conservación pelágica”. Game et al. (2009) [81] proporcionan una descripción general de muchos de los problemas, desafíos y posibles soluciones para las AMPPs. Dos de los grandes desafíos son la definición de AMPPs "específicas" y su implementación.

Por lo tanto, un alto conocimiento de la complejidad ecológica de los recursos pelágicos es esencial para la identificación de AMPP "específicas" adecuados [85]. Por ejemplo, Game et al. (2009) [81] observan que la definición de AMPP "específicas" puede ser problemática dada la falta de fidelidad al sitio de algunos animales pelágicos. Una forma de combatir la falta de fidelidad al sitio en los animales pelágicos es implementar AMP temporalmente variables [86]. Las distribuciones de los animales pelágicos son generalmente predecibles sobre la base de la comprensión de los factores ambientales [87,88]. En este sentido, las AMPs se definen mejor en función de características pelágicas importantes (por ejemplo, remolinos, frentes térmicos, células de surgencia, etc.), que a menudo tienen un alto grado de predictibilidad espacial o temporal [89,90]. Kaplan et al. 2010 [91] señalan que algunas especies pelágicas muestran los niveles de fidelidad al sitio requeridos para las “AMP objetivo”, esto no siempre es cierto. Por ejemplo, aunque las especies de túnidos de zonas templadas a menudo se agregan en aguas más cálidas para la reproducción [87], muchas especies de túnidos tropicales, como el listado *Katsuwonus pelamis* [88], no presentan migraciones claras de desove o alimentación.

En términos de su implementación, algunas de las acciones más importantes son los enfoques rentables, la coordinación y el conflicto entre múltiples agencias y el monitoreo de los AMPPs [85].

Estudio de caso: Parque Nacional Isla del Coco (Costa Rica)

A pesar de la protección legislativa que tienen las AMPs, se siguen planteando amenazas directas e indirectas para las especies vulnerables que se encuentran en las AMPs. Dentro de la propia AMP, las áreas con alta biodiversidad, hábitats preferentes y abundancia de especies más sensibles deben ser conocidas para proporcionar una vigilancia más activa. En este contexto, presentamos el estudio de caso del Parque Nacional Isla del Coco (PNIC).

Isla del Coco está ubicada en el Pacífico tropical oriental (N 05 ° 31´08´´, W 87 ° 04´18´´), 500 km al suroeste de la costa del Pacífico de Costa Rica a la que se llega solo después de un viaje en bote de 36 horas desde tierra firme [92]. La isla de 24 km^2 está rodeada por una plataforma insular que cubre un área de unos 300 km^2 e inicialmente se profundiza a unos 180 m antes de descender a varios miles de metros de profundidad [93-95]. Esta plataforma proporciona un hábitat excepcional para los organismos marinos debido a una combinación de características que incluyen el clima, la exposición a diversas corrientes oceánicas y la geología. Las aguas que rodean la isla tienen una termoclina permanente y poco profunda, caracterizada por una gran abundancia de zooplancton y peces pelágicos. Tales características explican que isla del Coco es un punto caliente de biodiversidad [96] teniendo la mayor biomasa de peces de los trópicos (7.8 toneladas / hectárea), de las cuales el 85% están representadas por depredadores ápice [97].

Isla del Coco fue declarada parque nacional en 1978, pero la parte marina no se incluyó hasta 1984. El parque fue declarado Patrimonio de la Humanidad por la UNESCO en 1997, y el área marina protegida se amplió en 1991 y nuevamente en 2001. El parque también es un sitio Ramsar desde 1998. En 2011, se creó un área de manejo especial alrededor del PNIC, el Área de Manejo Marino de los Montes Submarinos con un área marina protegida de 9.640 km2 [98].

Objetivo de estudio y esquema de trabajo.

Estudiamos el caso de una de las reservas marinas oceánicas más antiguas con el fin de evaluar cómo se distribuyen sus recursos, la pesca ilegal en el AMP y brindar una herramienta de planificación territorial para su gestión. El estudio se estructura en tres capítulos:

- Capítulo 1: Introducción. Marco de estudio.

- Capítulo 2: Patrones de abundancia y distribución de *Thunnus albacares* en el Parque Nacional Isla del Coco a través de Modelos Predictivos de Adecuación de Hábitat.

En este capítulo exploramos la distribución y abundancia del atún de aleta amarilla (*Thunnus albacares*) dentro del PNIC. Específicamente, evaluamos si los cambios en la distribución y abundancia de esta especie en el PNIC están relacionados con las características del hábitat, la intensidad de la pesca, los cambios en la temperatura promedio de la superficie del mar y los eventos El Niño-Oscilación Sur. En este estudio, utilizamos modelos espacio-temporales jerárquicos bayesianos para mapear los hábitats esenciales del atún aleta amarilla (*Thunnus albacares*) en las aguas alrededor del PNIC con base a observaciones submarinas realizadas de 1993 a 2013.

- Capítulo 3: Modelos predictivos de idoneidad de hábitat para ayudar a la conservación de elasmobranquios en el Parque Nacional Isla del Coco (Costa Rica).

Se estudian las preferencias de hábitat, la ecología espacial y se identifican puntos críticos para 12 especies de elasmobranquios (pelágicos y arrecife) dentro del PNIC con base a predictores ambientales. Dentro de este contexto, se realizaron modelos aditivos generalizados (GAM) para investigar las preferencias ambientales de ocho especies de elasmobranquios entre seis predictores (temperatura de la superficie del mar, salinidad, concentración de clorofila-a, batimetría, distancia de la costa y talud) en el PNIC. Así mismo, también se realizó un análisis clúster con el fin de verificar si las ocho especies estudiadas son representativas de toda la comunidad de elasmobranquios estudiada en esta área. Si los resultados de análisis clúster muestran un alto grado de similitud entre el conjunto de especies de las diferentes inmersiones, se supone que los hábitats sensibles identificados para las once especies estudiadas son compartidos por las especies de elasmobranquios restantes. En consecuencia, la conservación de estos hábitats contribuiría en gran medida a proteger a toda la comunidad de elasmobranquios en esta área.

- Capítulo 4: Pesca ilegal en el Parque Nacional Isla del Coco: distribución espacio-temporal y compensaciones económicas.

En este capítulo, modelamos la distribución espacial de la pesca ilegal en relación a variables topográficas, biológicas y temporales con el fin de obtener una distribución espacio-temporal de la pesca ilegal y predecir áreas que podrían ser propensas a la pesca ilegal pero que actualmente no se detectan. Además, queremos obtener información sobre las áreas más rentables para esta actividad y la compensación económica por esta actividad ilegal en relación a los posibles beneficios y costes. Para ello, analizamos un conjunto de datos que cubre 8 años (2003-2010) de registros de patrullas del PNIC mediante Modelos Aditivos Generalizados Auto-covariados Residuales (RAC-GAM).

En esta tesis aplicamos un marco analítico a través de datos georreferenciados y análisis estadístico de especies sensibles y pesquerías pelágicas ilegales. Este enfoque proporciona información básica y esencial para evaluar los diferentes niveles de presión de la pesca ilegal y profundizar la comprensión de la distribución y preferencia de hábitat de especies de importancia ecológica y comercial. Un conocimiento sólido de esta información es un requisito fundamental para gestionar los recursos de forma eficiente, sostenible y es una herramienta útil para la ordenación del territorio. Por lo tanto, esta herramienta puede ser la base para el diseño de programas integrados de gestión más eficiente de especies vulnerables.

Discusión general

La protección de los ecosistemas pelágicos será fundamental para alcanzar los objetivos mundiales de conservación marina, como los del Convenio sobre la Diversidad Biológica, que pide proteger el 10% de los océanos del mundo a través de AMP para 2020 (Convenio sobre la Diversidad

Biológica 2010). Para alcanzar estos objetivos, ha habido una tendencia creciente en los últimos años a crear AMPP a gran escala, en su mayoría pelágicas [99]. Estos AMPP pueden ser lo suficientemente grandes como para protegerse contra amenazas e incorporar partes clave de hábitats y movimientos de animales de gran alcance o migratorios [100-103].

Sin embargo, muchas AMPP han sido designadas recientemente o están en etapas de desarrollo, y muy pocos han existido el tiempo suficiente para extraer lecciones relevantes para el manejo de AMPP en otros lugares. A pesar del fuerte aumento en el número de AMPP, existe poca literatura sobre enfoques en el terreno para su gestión, en gran parte debido a la relativa novedad de muchos AMPPs a gran escala.

Por tanto, los principales retos de gestión de los AMPPs son los objetivos, el seguimiento y el cumplimiento [104]. La naturaleza dinámica de los ambientes pelágicos presenta desafíos únicos para la gestión. La aplicación de las AMPPs puede resultar particularmente difícil debido a las áreas extensas y a menudo remotas que se deben monitorear y al coste para llegar a estas áreas [105]. Además, se debe considerar la rentabilidad, la coordinación de múltiples gestores y las amenazas más allá de los límites del AMPP.

Aunque los objetivos del AMPPs pueden variar, el mantenimiento del sistema ecológico y la protección de especies vulnerables son prioridades comunes. Establecer prioridades biológicas para el seguimiento y la aplicación significa determinar dónde es probable que se encuentren las especies o hábitats más vulnerables y cuándo son más vulnerables [106].

La priorización biológica se basa en datos de referencia de especies y hábitats clave, así como de usos e impactos humanos. Sin embargo, la integración de datos clave sobre especies, hábitats y uso humano (por ejemplo, pesca ilegal) determinará dónde coexisten las regiones de mayor amenaza e importancia ecológica [107-109]. En este paso es particularmente importante considerar dónde ocurren estas áreas tanto temporal como espacialmente.

Para lograr estos objetivos, los modelos de hábitat y mapas predictivos, como los generados por el enfoque presentado en esta tesis, podrían ser una fuente de información útil en la selección de áreas para una mejor gestión regional o adopción de medidas técnicas. Creemos que el uso de este enfoque para la construcción de mapas de la distribución espacial de especies vulnerables puede ayudar al diseño de programas integrados para la gestión y el control más eficiente de los recursos marinos.

En particular, en esta tesis se utilizaron dos tipos de conjuntos de datos, las observaciones submarinas y los datos de pesca ilegal obtenidos por los guardaparques. Los datos de las observaciones subacuáticas recopiladas por los centros de buceo pueden representar una de las fuentes de datos más importantes, pero a menudo subestimadas, para estudiar los recursos marinos en lugares donde la pesca está prohibida. Los datos de las observaciones submarinas fueron utilizados para mejorar nuestra comprensión de la utilización del hábitat por los elasmobranquios y el atún de aleta amarilla (*Thunnus albacares*) en PNIC.

En general, nuestros resultados ayudaron a evaluar la influencia del medio ambiente en el atún de aleta amarilla (*Thunnus albacares*) y en la mayoría de las especies que constituyen la comunidad de elasmobranquios de la isla. Además, se identificaron los hábitats preferenciales de estas especies.

Los datos de pesca ilegal ayudaron a comprender la distribución espacio-temporal de esta actividad y a obtener importantes resultados predictivos como detectar otras áreas que pueden ser propensas a la pesca ilegal pero que actualmente no se detectan. Estos posibles lugares identificados de actividad pesquera ilegal deben ser monitoreados de cerca para prevenir la actividad ilegal antes de que suceda. Además, en el cuarto capítulo se evaluó la compensación económica de esta actividad ilegal en relación con las ganancias potenciales y los costos. Se estima que esta actividad ilegal continuará en el tiempo porque los beneficios potenciales superan los costos potenciales de ser capturados. Esto nos lleva a pensar que poner sanciones más altas podría contribuir a desalentar esta actividad.

En general, debe tenerse en cuenta que en nuestro estudio los datos ambientales y de especies fueron muestreados durante un período limitado de tiempo y espacio y, por lo tanto, los modelos ajustados solo pueden reflejar una imagen instantánea de la relación esperada entre el medio ambiente y las especies analizadas. Los estudios futuros deberían comparar la distribución espacial de estas especies con una serie de tiempo más larga y combinando otras fuentes de datos. Sin embargo, los resultados de esta tesis podrían servir para promover un mayor esfuerzo en la recolección de datos en las áreas identificadas en las que deben enfocarse los futuros intentos de investigación. Por estas razones, son necesarios estudios similares sobre la distribución de elasmobranquios y otras especies vulnerables que cubren otras épocas del año (estaciones) para apoyar los planes de conservación en esta área.

Conclusiones

Con los datos disponibles, los principales predictores de los hábitats de elasmobranquios en el PNIC fueron la distancia a la costa, la pendiente y la clorofila-a, lo que indica que los elasmobranquios prefieren aguas poco profundas cerca de la isla y con diferentes grados de pendiente del fondo marino.

El atún aleta amarilla (*Thunnus albacares*) mostró una tendencia a disminuir en abundancia durante el período de muestreo. Las mayores abundancias se encontraron en aguas someras y cálidas, con una alta concentración de clorofila-a, y en los montes submarinos circundantes influenciados por la topografía y estructura del fondo marino.

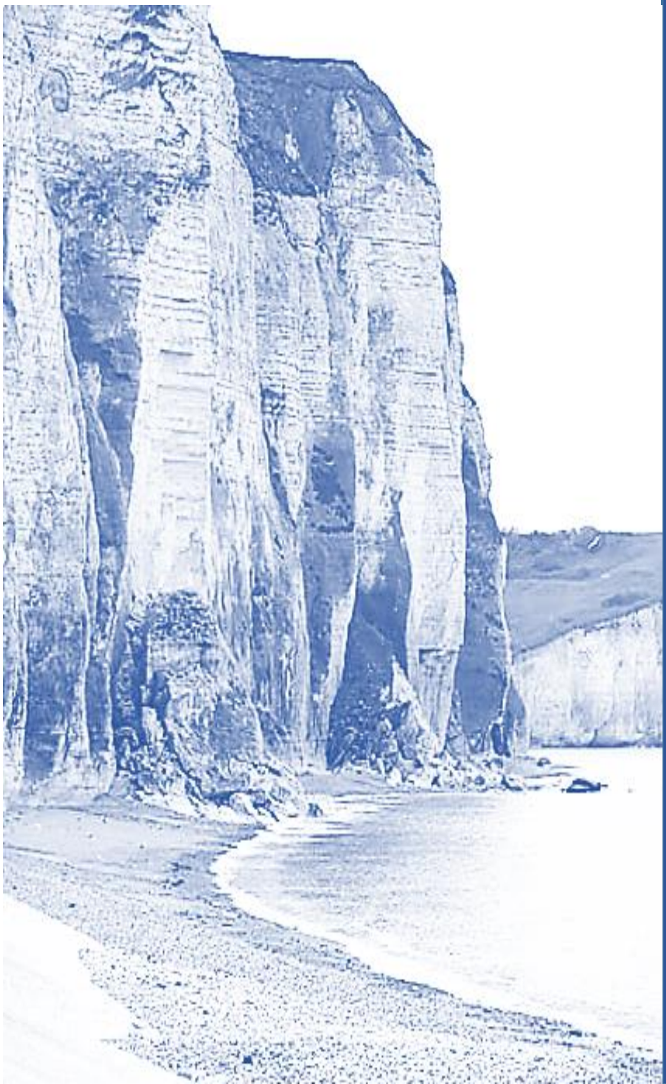
En cuanto a la pesca ilegal de elasmobranquios y atún de aleta amarilla, los principales factores que influyen en la distribución de la pesca ilegal fueron la batimetría del fondo marino, la pendiente y abundancia de atún de aleta amarilla (*Thunnus albacares*) y tiburones. Los mapas predictivos sugieren una tendencia importante de pesca ilegal entre el segundo y el tercer trimestre del año en las aguas que rodean un monte submarino dentro del Parque. Los mapas de las áreas más rentables destacaron una ubicación de riesgo específica que debe ser monitoreada de cerca. En general, los beneficios potenciales de esta actividad superan los costos potenciales de ser capturados y por lo tanto se estima que esta actividad ilegal continuará en el tiempo.

Por último, queremos señalar, que creemos que no existen soluciones a corto plazo. Para restaurar las pesquerías globales y hacer un uso sostenible del medio marino, es necesario comprender la ecología de las especies vulnerables y las consecuencias ecológicas de la explotación para hacer una adecuada gestión de los ecosistemas marinos. Es imprescindible respetar la integridad ecológica de los ecosistemas explotados para garantizar su funcionamiento y sostenibilidad, y diseñar planes de gestión en base a las especies más sensibles a la explotación pesquera. Cualquier medida y diseño de AMP pasa por conocer los hábitats sensibles y la ecología de la especie o especies en cuestión.

Los modelos de hábitat y mapas predictivos podrían ser una fuente de información útil para alcanzar el conocimiento necesario en la selección de áreas para el establecimiento de AMP y su gestión. Este conocimiento junto a la comprensión de la biología de la especie son la base para garantizar la biodiversidad, la estructura del ecosistema marino, sostenibilidad de la pesca y, por consiguiente, seguridad alimentaria.

Chapter 1:

Introduction



Introduction

1.1. Status of global fisheries: Large pelagics and reef elasmobranchs

Fishery resources have shown a gradual and constant deterioration in the last decades [1-5]. According to FAO (SOFIA 2018), the part of fish stocks that are within biologically sustainable levels has shown a downward trend from 90% in 1974 to 66.9% in 2015 and the percentage of stocks exploited at levels biologically unsustainable increased from 10% in 1974 to 33.1% in 2015. Fishing overexploitation has also affected large pelagic predator fisheries (sharks, tunas, and billfish) around the world [6-10]. This global effect has reached even the most remote parts of the ocean as the well-known "sanctuaries" [6].

Large predators play a critical role in the marine ecosystem [11] maintaining complex ecosystems by providing food sources for scavengers [12] and regulating the size and dynamics of prey populations by eliminating weak individuals [13,14]. The selective elimination of predators can lead to changes in trophic interactions [4,15,16] reflected at the community level.

Some predator species are especially sensitive to overexploitation, in particular elasmobranchs, which due to their biological characteristics (longevity, few progeny and late sexual maturation) cannot sustain high mortality [17-19].

It is currently estimated that large predator populations have decreased by 90% during the last 50 years, prior to industrial exploitation [6,20]. According to the United Nations Convention on Highly Migratory Fish Stocks, May 2006 [21] global longline fishing in the high seas must be significantly reduced to reverse the process of depletion of tuna, sharks, and other fish stocks. If the decline continues, the extinction of sensitive populations and species is a real threat. Different studies have confirmed the disappearance of elasmobranchs. Aldebert, (1998) [22] indicates the disappearance of 14 species of elasmobranchs from the Gulf of the Lions (northwestern Mediterranean) and according to Quero, (1998) [23] nine species of elasmobranchs have disappeared from the Bay of Biscay (Cantabrian Sea) between 1957 and 1995.

Specifically, overfishing of yellowfin tuna and sharks is encouraged by the high economic value in national and international markets [24,25] both for their meat and for their by-products: shark liver, skin and fin oil [26,27].

Thus, overfishing, together with habitat degradation and changes in marine systems, directly alter the composition of ecological communities and the structure and productivity of marine systems [28].

1.1.1. Situation of the pelagic fishery in Costa Rica

Costa Rica has multiple threats to its marine resources. In general terms, it is observed that the levels of fishing production have been maintained as a result of the increase in the capture of non-traditional pelagic species, such as shark, dolphinfish (*Coryphaena hippurus*) and tuna [29 -31]. Furthermore, the fishing effort (number of boats, number of hours at sea) has increased and a reduction of the traditional resource is observed, such as croaker (*Pseudosciaena crocea*), snook (*Centropomus undecimalis*), snapper (*Pagrus auratus*) and conger eel (*Conger sp*) [32, 33].

Large pelagics have exceeded their maximum sustainable yield, showing reductions of 22% in pelagic resources landed in the country [34]. Specifically, the capture of elasmobranchs shows signs of depletion with decreases of 60% in their relative abundance between 1991 and 2001 [35,36].

Yellowfin (*Thunnus albacares*) tuna and bigeye tuna (*Thunnus obesus*), key resources for the national industry, are also in trouble due to overfishing, showing a serious deterioration in the state of their population [35,37]. According to the Inter-American Tropical Tuna Commission (2004) [37], the tunas currently caught are very small, well below the recommended size for maximum sustainable production.

1.2. Offshore MPAs: Oceanic islands and seamounts.

1.2.1. General characteristics of oceanic islands and seamounts

In general, seamounts located in shallow waters and oceanic islands are areas of high occurrence for pelagic biota [38-43] being hotspots of high biodiversity. These associations of pelagic species with seamounts have been previously described for some species of tunas [43-45], sharks [42,46] (Figs.1,2), and billfishes [47,48]. Thus, seamounts and oceanic islands are critical points for pelagic biodiversity, and may be suitable areas for the conservation of ocean ecosystems [49].

Fig. 1. Scalloped hammerhead (*Sphyrna lewini) in* PNIC.

Fig. 2. Whitetip reef shark (*Triaenodon obesus*) in PNIC.

These areas can create conditions such as increased vertical nutrient fluxes and material retention that promote productivity feeding different trophic levels [50-52] such as pelagic predators (sharks and tunas) [53,54]. In addition, these areas also provide rest stops and cleaning stations [43]. These combinations of factors make seamounts and oceanic islands suitable mating, feeding and nursery grounds for highly migratory pelagic species as well as benthic organisms [55].

1.2.2. MPAs *applied to the protection of large pelagics.*

Pelagic ecosystems face a number of threats including overfishing, pollution, climate change, ocean acidification, shipping, eutrophication, and species introductions [56]. Protecting pelagic ecosystems will be critical to meeting global marine conservation targets, such as the Convention on Biological Diversity's (CBD) call to protect 10% of the worlds' oceans through marine protected areas (MPAs) by 2020 (Convention on Biological Diversity 2010) [57].

Open ocean ecosystems can be protected by identifying biodiversity hotspots [6,49] as potential locations for offshore marine reserves [20,58]. The pelagic marine protected areas (PMPAs) may be large enough to guard against threats and incorporate key portions of far-ranging or migratory animal habitats and movements) [59-,61].

Fig. 3. The Biological Corridor of the Eastern Pacific.

It is important to mention that the dynamism of pelagic environments can significantly reduce the effectiveness of conservation measures [62]. Thus, it is necessary to create a network of Marine Protected Areas (MPAs), or temporarily and spatially closed areas, in areas of breeding, migration, and reproduction of sensitive or commercially exploited species. This network of MPAs is essential to protect pelagic biodiversity and achieve sustainability of marine predator species [62]. We can point out as an example of such an initiative "The Biological Corridor of the Eastern Pacific" signed in April 2004, in San José (Costa Rica) by the governments of Colombia, Ecuador, Costa Rica and Panama (Fig. 3), This “corridor” is formed by the Oceanic Islands of Galapagos (Ecuador), Cocos (Costa Rica), Coiba (Panama), Malpelo and Gorgona (Colombia).

Game et al. (2009) [59] argue that “recent advances in conservation science, oceanography and fisheries provide the evidence, tools and information to ... confirm that PMPAs are defensible and feasible instruments for pelagic conservation”. Game et al. (2009) [59] provide an overview of many of the problems, challenges, and possible solutions for PMPAs. Two of the big challenges are the definition of "specific" PMPAs and their implementation.

Therefore, a high understanding of the ecological complexity of pelagic resources is essential for the identification of suitable "specific" PMPAs [63] (Maxwell et al. 2014). For example, Game et al. (2009) [59] note that the definition of "specific" PMPAs may be problematic given the lack of site fidelity of some pelagic animals. One way to combat the lack of site fidelity in pelagic animals is to implement temporally variable MPAs [64]. The distributions of pelagic animals are generally predictable based on an understanding of environmental factors [65,66]. In this sense, MPAs are better defined based on important pelagic characteristics (eg eddies, thermal fronts, upwelling cells, etc.), which often have a high degree of spatial or temporal predictability [67,68]. Kaplan et al. 2010 [69] notes that some pelagic species show the levels of site fidelity required for the “target MPAs”, this is not always true. For example, although temperate tuna species often aggregate in warmer waters for reproduction [65], many tropical tuna species, such as skipjack *Katsuwonus pelamis* [66], do not exhibit clear spawning or feeding migrations.

In terms of its implementation, some of the most important actions are cost-effective approaches, coordination and conflict between multiple agencies, and monitoring of PMPAs [63].

1.3. Case study: Isla del Coco National Park (Costa Rica)

Despite the legislative protection that MPAs have, it continues to pose direct and indirect threats to vulnerable species found in MPAs. Within the MPA itself, areas with high biodiversity, preferred habitats, and abundance of more sensitive species should be known to provide more active surveillance. In this context, we present the case study of the Isla del Coco National Park (PNIC) (Costa Rica).

PNIC, Costa Rica, is located 550 km southwest of the Pacific coast of Costa Rica [70]. The organisms and marine environments of Cocos Island were described by explorers from the end of the XVII to the present [71,64] (Fig. 4).

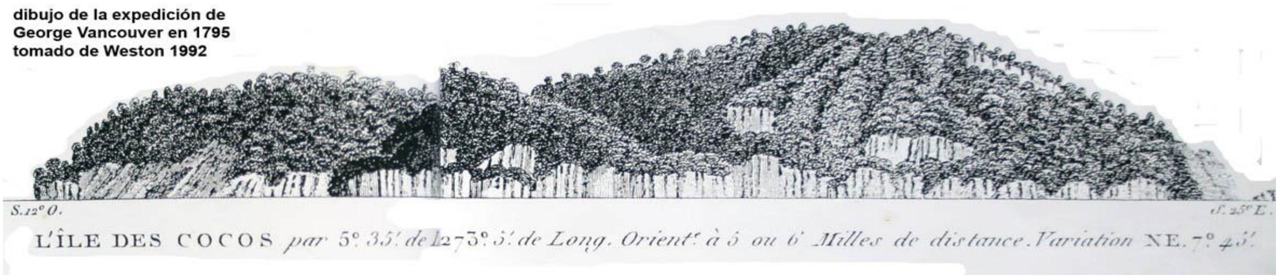


Fig. 4. Picture of PNIC at 1795.

The island is a biodiversity hot-spot [72], due to a combination of features including climate, exposure to diverse ocean currents, and geology. The waters surrounding the island have a permanent and shallow thermocline, characterized by a high abundance of zooplankton and pelagic fish. Such features explain why Isla del Coco has the highest fish biomass in the tropics (7.8 tonnes/hectare), of which 85% are represented by apex predators [73]. Isla del Coco was declared a national park in 1978 but the marine portion was only included in 1984. The park was declared a UNESCO World Heritage site in 1997, and the marine protected area was extended in 1991 and again in 2001. The park is also a Ramsar site since 1998. In 2011, a special management area was created around PNIC, the Seamounts Marine Management Area with a marine protected area of 9,640 km2 [74].

1.3.1. Study objective and work scheme.

We study the case of one of the oldest oceanic marine reserves (PNIC) in order to evaluate how its resources and illegal fishing are distributed in the MPA and to provide a territorial planning tool for its management. The study is structured in three chapters:

- Chapter 1: Introduction. Study framework.

- Chapter 2: Abundance and Distribution Patterns of *Thunnus albacares* in Isla del Coco National Park through Predictive Habitat Suitability Models.

We explored the distribution and abundance of yellowfin tuna within the PNIC. Specifically, we evaluate whether the changes in the distribution and abundance of this species in the PNIC are related to the characteristics of the habitat, the intensity of fishing, the changes in the average temperature of the sea surface and El Niño-Southern Oscillation events.

- Chapter 3: Predictive habitat suitability models to aid the conservation of elasmobranchs in the Isla del Coco National Park (Costa Rica).

We studied habitat preferences, spatial ecology, and identified hotspot areas of 12 elasmobranch species (pelagic and reef) within the PNIC based on environmental predictors.

- Chapter 4: Illegal fishing in Isla del Coco National Park: spatial-temporal distribution and the economic trade-offs.

In this chapter, we model the spatial distribution of illegal fishing activity in relation to topographic, biological and temporal variables in order to obtain a spatio-temporal distribution of illegal fishing and predict areas that could be prone to illegal fishing but that are currently not detected. In addition, we want to obtain information on the most profitable areas for this activity and the economic compensation for this illegal activity in relation to the potential profits and costs.

In this thesis we applied an analytical framework through georeferenced data and statistical analysis of sensitive species and illegal pelagic fisheries. This approach provides basic and essential information to assess the different levels of illegal fishing pressure and to deepen the understanding of the distribution and habitat preference of species of ecological and commercial importance. A solid knowledge of this information is a fundamental requirement to manage resources efficiently, sustainably and is a useful tool for spatial planning. Thus, this tool can be the basis for the design of integrated programs for more efficient management of vulnerable species.

Chapter 2: Abundance and Distribution Patterns of *Thunnus albacares* in Isla del Coco National Park through Predictive Habitat Suitability Models

Abundance and distribution patterns of *Thunnus albacares* in Isla del Coco National Park through predictive habitat suitability models.

2.1. Abstract

Information on the distribution and habitat preferences of ecologically and commercially important species is essential for their management and protection. This is especially important as climate change, pollution, and overfishing change the structure and functioning of pelagic ecosystems. In this study, we used Bayesian hierarchical spatial-temporal models to map the Essential Fish Habitats of the Yellowfin tuna (*Thunnus albacares*) in the waters around Isla del Coco National Park, Pacific Costa Rica, based on independent underwater observations from 1993 to 2013. We assessed if observed changes in the distribution and abundance of this species are related with habitat characteristics, fishing intensity or more extreme climatic events, including the El Niño Southern Oscillation, and changes on the average sea surface temperature. Yellowfin tuna showed a decreasing abundance trend in the sampled period, whereas higher abundances were found in shallow and warmer waters, with high concentration of chlorophyll-a, and in surrounding seamounts. In addition, El Niño Southern Oscillation events did not seem to affect Yellowfin tuna distribution and abundance. Understanding the habitat preferences of this species, using approaches as the one developed here, may help design integrated programs for more efficient management of vulnerable species.

2.2. Introduction

Pelagic ecosystems are undergoing extreme changes in their structure and functioning due to climate change, pollution and overfishing [1]. Fisheries, for example, now access and exploit remote areas, such as deep ocean habitats, as closer and more traditional fishing grounds get depleted [2].

Marine top predators, including marine mammals, sharks, large tuna and billfish, are declining worldwide at a rapid rate, which can largely be attributed to fisheries [3]. The loss of these taxa is expected to have important effects in pelagic ecosystems, influencing many other organisms throughout the food chain and their associated habitats [4]. While different management tools, such as Marine Protected Areas (MPAs), have been increasingly used to protect benthic species and habitats in coastal waters (e.g.: coral reefs) [5], the protection of pelagic ecosystems and top-predators has been widely overlooked, expect for a few examples [6]. This is mostly due to the intrinsic dynamics of these habitats and the high mobility of these species. MPAs specifically designed to protect the pelagic environment would be harder to enforce and systematically monitor, due to the remoteness of the majority of the pelagic ecosystems. Despite such difficulties, there are a few examples of MPAs that were established, intentionally or not, with the goal of protecting pelagic species.

Isla del Coco National Park, Costa Rica, is one of these examples. It is an uninhabited island, located 550 km southwest of the Pacific coast of Costa Rica, reached only after a 36h boat ride from the mainland. Isla del Coco was declared a national park in 1978 but the marine portion was only included in 1984. The park was declared a UNESCO World Heritage site in 1997, and the marine protected area was extended in 1991 and again in 2001. The park is also a Ramsar site since 1998. In 2011, a special management area was created around Isla del Coco National Park, the Seamounts Marine Management Area with a marine protected area of 9,640 km^2 [7].

The island is a biodiversity hot-spot [8], due to a combination of features including climate, exposure to diverse ocean currents, and geology. The waters surrounding the island have a permanent and shallow thermocline, characterized by a high abundance of zooplankton and pelagic fish. Such features explain why Isla del Coco has the highest fish biomass in the tropics (7.8 tonnes/hectare), of which 85% are represented by apex predators [9].

Although Isla del Coco has been protected and monitored for over 20 years [10], illegal fishing of large pelagic species still occurs within the park's limits [11]. Legal and illegal fisheries of these species are difficult to monitor all over Costa Rica's Exclusive Economic Zone. A significant source of uncertainty follows from the fact that large foreign fishing fleets operate in the region [12], with foreign markets driving the demand [13]. Official data show that from 1990 to 2000s fishing fleets in Costa Rica have rapidly grown, with an increase in landings from around 18,000 to 34,500 $t \cdot year^{-1}$ [14]. The ratio of coastal (fishes and crustaceans) to pelagic (tunas and billfishes) landings changed from 3:2 to 1:4 [12]. Catches of large pelagic species have increased during the last decade, and currently they are about 50% of the reported landings.

Fishing fleets of Costa Rica catch five species of tuna, with the Yellowfin tuna (*Thunnus albacares*) making up the majority of the catch (84.97%) [15]. This large pelagic species [16, 17] is globally distributed over the tropical and subtropical oceans [18], and its distribution in the Eastern Tropical Pacific ranges from southern California USA, to Peru [19]. Yellowfin tuna have extremely large population sizes compared to other tunas and its migration occurs between the Atlantic and Indo- Pacific Oceans [19]. In addition, it is listed as "Near threatened" and "trend decreasing" by the IUCN Red List [20].

In this study, we explored the distribution and abundance of the Yellowfin tuna within the Isla del Coco MPA from 1993 to 2013, using visual census data. Specifically, we assessed if changes in the distribution and abundance of this species in the MPA are related with habitat characteristics, fishing intensity and climate, including El Niño-Southern Oscillation (ENSO) events and longer-term changes in the average sea surface temperature [21].

2.3. Material and methods

2.3.1. Yellowfin tuna data

The Undersea Hunter Group [22] is a private diving company that operates in Isla del Coco and has one of the longest underwater visual censuses (UVC) for Yellowfin tuna, among others species, in the Eastern Tropical Pacific. Dives were performed between January 1993 and December 2013 at 17 different sites around Isla del Coco, resulting in 27,261 immersions (Fig. 1 and Table 1).

Each dive, always led by an experienced Divemaster during day light, averaged ~60 min and ranged in depth between 10-40 m. A total of 25 Divemaster led the dives along the time series. Although the dive protocol was not entirely standardized as in a scientific underwater visual census, the protocol was consistent throughout the period [21]. The maximum number of fish seen throughout the dive was recorded only when there were fewer than 100 individuals, whereas estimates were used otherwise (e.g., for schools of 1000 or more tunas).

Fig. 1. Map of the study area and the dive locations.

Possible biases of false absences, which occur when an observer fails to record a present species, and recounting of individuals may have occurred during dives, however, such error would have been consistent throughout the survey period. In addition, as already demonstrated by White *et al.* (2015) [10], data collected by Divemasters can be a reliable way to discern trends in relative abundance, especially for large pelagic species that are easily identified [23].

Data were aggregated by year after excluding seasonality patterns with the Autocorrelation (ACF) and Partial Autocorrelation Function (PACF) in the R software [24].

Table 1. Summary of the number of dives for location and year around the island from the 1993 to 2013.

		1993	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	
North	I. Manuelita	103	90	124	138	75	167	345	344	256	523	410	298	531	519	608	543	549	624	901	723	630	
	Chatham B.	0	1	2	0	0	4	1	3	2	8	12	22	25	45	50	56	56	63	10	18	131	
	Lobster R.	17	17	18	20	15	54	56	36	31	72	69	24	53	62	59	46	84	58	117	136	137	
	Silverado	0	0	0	0	0	3	66	55	55	7	74	59	97	88	102	119	85	61	26	13	5	
		120	**108**	**144**	**158**	**90**	**228**	**468**	**438**	**344**	**610**	**565**	**403**	**706**	**714**	**819**	**764**	**774**	**806**	**1054**	**890**	**903**	**11106**
West	I. Pajora	1	1	9	23	5	11	25	38	24	51	43	34	73	56	48	47	67	56	80	82	81	
	Viking Rock	20	17	9	13	8	19	43	38	30	89	63	62	58	64	99	50	45	40	91	77	71	
	Wafer B.	0	0	0	0	0	0	1	2	0	5	5	2	3	14	13	7	8	5	12	12	7	
	Dirty Rock	110	90	102	117	62	128	177	175	166	291	238	159	243	264	268	240	298	315	363	369	315	
	Maria P.	0	0	0	12	10	37	57	78	36	80	49	40	89	98	132	89	136	134	241	222	192	
		131	**108**	**120**	**165**	**85**	**195**	**303**	**331**	**256**	**516**	**398**	**297**	**466**	**496**	**560**	**433**	**554**	**550**	**787**	**762**	**666**	**8179**
East	Manta C.	12	4	1	5	0	10	7	3	3	15	10	2	8	2	4	6	5	2	8	1	1	
	Iglesias B.	0	0	0	0	1	3	0	2	1	1	4	1	0	0	1	4	1	0	0	8	0	
	Submerged R.	20	19	13	23	16	30	50	54	35	66	55	37	52	65	53	70	71	62	76	82	85	
	Alcyone	19	27	23	34	39	133	128	132	150	243	236	137	230	210	239	230	273	285	349	366	291	
		51	**50**	**37**	**62**	**56**	**176**	**185**	**191**	**189**	**325**	**305**	**177**	**290**	**277**	**297**	**310**	**350**	**349**	**433**	**457**	**377**	**4944**
South	Bajo Dos Amigos	3	2	1	2	5	22	3	1	6	35	3	0	0	0	6	8	0	1	0	2	0	
	Big Dos Amigos	20	18	11	20	10	34	30	49	37	53	51	34	77	78	56	70	75	58	92	81	61	
	Small Dos Amigos	6	3	2	13	13	49	40	65	64	120	90	45	91	91	59	76	70	57	96	92	53	
	Lone Stone	25	17	20	24	21	61	57	64	39	91	41	22	56	29	17	25	45	12	27	22	7	
		54	**40**	**34**	**59**	**49**	**166**	**130**	**179**	**146**	**299**	**185**	**101**	**224**	**198**	**138**	**179**	**190**	**128**	**215**	**197**	**121**	**3032**
	Total	356	306	335	444	280	765	1086	1139	935	1750	1453	978	1686	1685	1814	1686	1868	1833	2489	2306	2067	

In order to assess possible trends in catches, landing data of Yellowfin tuna were extracted for the time series 1993-2010. These data were available for all of Costa Rica’s Exclusive Economic Zone (EEZ) from the *Sea Around Us* website [25]. Landings are “reconstructed data” that combine official reports of the Food and Agriculture Organization of the United Nations (FAO) [14] and reconstructed estimates of Illegal, unreported and unregulated (*IUU*) fisheries data [26,27].

2.3.2. Environmental data

Six environmental variables were considered as potential predictors of Yellowfin tuna abundance, including three climatic variables –Sea Surface Temperature (SST), sea surface salinity (SSS) and Chlorophyll-a concentration (Chl-*a*) – and three bathymetric features – depth, slope and distance to coast.

Bathymetric features were derived from the MARSPEC database [28]. MARSPEC is a world ocean dataset with a spatial resolution of 0.01 x 0.01 degrees developed for marine spatial ecology [29].

Depth and distance to coast are some of the main factors controlling species distribution and have been identified as predictors to determine spatial patterns of many species and in particular Yellowfin tuna [30, 31]. Slope is an index of seabed morphology and has been used as predictor of species distribution and of suitable habitats [32–35]. Low values of slope correspond to a flat ocean bottom (or areas of sediment deposition) while higher values indicate potential rocky ledges [33].

SST and Chl-*a* variables were extracted from different sensors as nightly monthly means and aggregated in yearly maps using the *Spatial Analysis* tool of ArcGIS 10 (Table 2).

As no exhaustive and validated time series of SSS was available, the climatology of monthly SSS was downloaded from the World Ocean Database 2013 (WOA13) (Table 2).

Table 2. Predictor variables used from modeling the abundance of the Yellowfin tuna in the Isla del Coco. SST =Sea Surface Temperature, SSS = Sea Surface Salinity, Chl-a = Chlorophyll-a.

Variable	Temporal resolution	Sensor	Platform
SST (°C)	1993-2006	AVHRR Pathfinder	www.neo.sci.gsfc.gov
SST (°C)	2007-2013	MODIS-Aqua	www.neo.sci.gsfc.gov
SSS	1993-2013	Standard Level Data: CTD (Surface)	World Ocean Database 2009
Chl-a (mg.m $^{-3}$)	1993-1996	NEMO climatology model	http://www.nemo-ocean.eu/
Chl-a (mg.m $^{-3}$)	1997-2013	SeaWiFS & MODIS-Aqua	http://oceancolor.gsfc.nasa.gov
Bathymetry (m)	-	SRTM30_Plus Bathymetry	www.marspec.org
Distance (km)	-	GSHHS Coastline	www.marspec.org
Slope (%)	-	Bathymetry	www.marspec.org

Salinity and SST are strongly related to marine system productivity as they can affect nutrient availability, metabolic rates and water stratification [36]. Yearly maps of the SST can indicate temperature variations due to ENSO events, which happened in this area in 1997-1998, 2006-2007 and 2012 [37, 38].

Chl-*a* concentration was included in the analysis as an index of primary production of an ecosystem [39, 40]. Several studies have showed that primary production is an important factor that drives the Yellowfin tuna abundance and distribution [18, 41].

All environmental variables were aggregated with a spatial resolution of 0.01 x 0.01 degrees. These variables were explored for collinearity, outliers, and missing data before their use in the models [42]. The variable distance to coast was highly correlated to depth (Pearson´s correlation, $r > 0.75$, p-value = 0.01) (Fig 2) and Chl-a (Pearson´s correlation, $r > 0.8$, p-value = 0.02), and thus, these variables were used alternatively in the models. Finally, to facilitate visualization and interpretation, the explanatory variables were standardized (difference from the mean divided by the corresponding standard deviation).

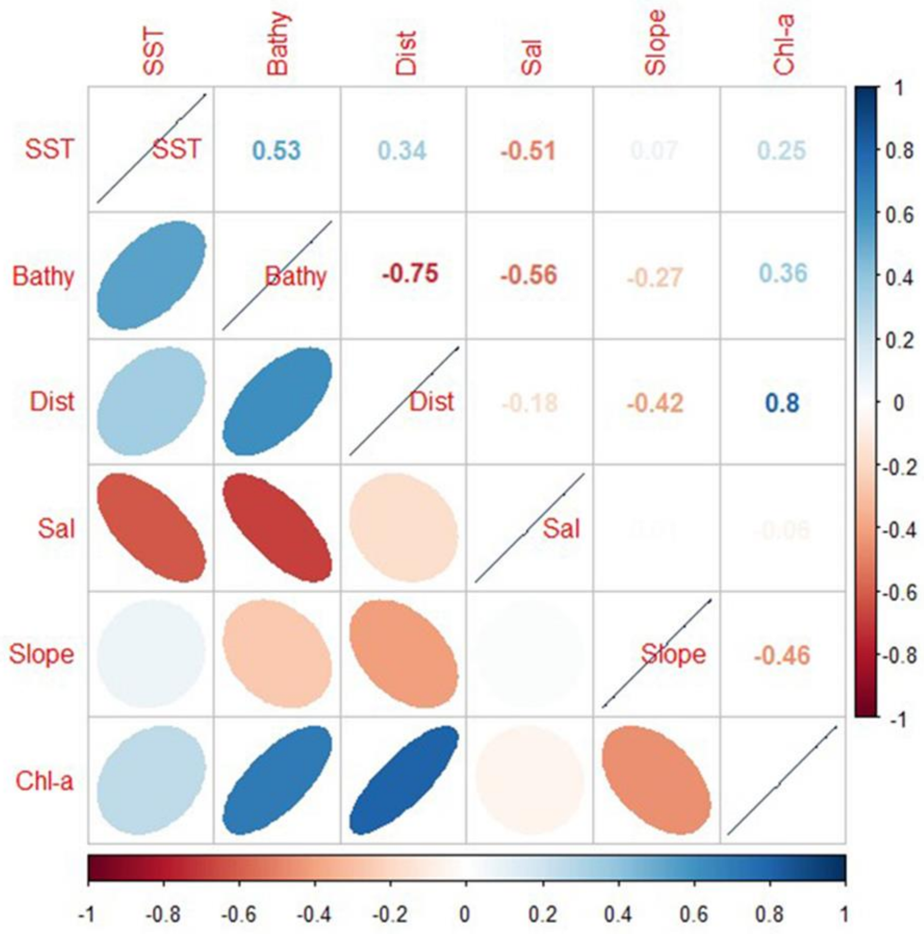


Fig. 2. Cross-correlation matrix of the environmental variables included in the model.

Finally, the Multivariate ENSO Index (MEI) was extracted from the NOAA website for the entire time series (2003-2013) (http://www.esrl.noaa.gov/). The Pearson and Spearman's correlations were computed between the MEI index and the Yellowfin tuna abundance in order to explore its effect on the species distribution. This index could not be included in the model because it does not have a spatial structure.

2.3.3. Statistical models and model validation

We used hierarchical Bayesian hierarchical hurdle model to investigate how Yellowfin tuna spatial-temporal distribution and abundance respond to the explanatory variables. These types of models are implemented to deal with high numbers of zero in dives, in two stages: (i) modeling presence/absence in order to obtain the envelope of the predicted probability of presence of the species studied and (ii) modeling the number of individuals (*i.e.*, count data) of the studied species only in areas where species were predicted to be present [43]. The first stage was modeled using a binomial distribution and the second with a Poisson distribution.

For both stages, the candidate explanatory variables included all environmental variables, the unstructured random effect of the year, a spatially structured random effect, an observer random effect and all possible interaction terms. The observer random effect is included in the model to account for a possible non-independence in the observations that could explain the remaining potential source of variation in the number of Yellowfin tuna sighted, due to the observers themselves (e.g.: personal experience) or due to unobserved survey characteristics (e.g.: water visibility). Finally, in order to account for the sampling effort variability among dive locations and year an offset was included in the second stage of the model. A vague zero-mean Gaussian prior distribution with a variance of 100 was used for all of the parameters involved in the fixed effects, while for the spatial effect a zero-mean prior Gaussian distribution with a Matérn covariance structure was assumed (see Muñoz et al. 2013 [44] for more detailed information about spatial effects).

For each particular parameter, a posterior distribution was obtained. Unlike the mean and confidence interval produced by classical analyses, this type of distribution enables explicit probability statements about the parameter. Thus, the region bounded by the 0.025 and 0.975 quantiles of the posterior distribution has an intuitive interpretation: for a specific model, the unknown parameter is 95% likely to fall within this range of values.

Once the inference has been carried out, we predicted the species abundance in the rest of the area of interest for the entire year using Bayesian kriging, which allows for the incorporation of parameter uncertainty into the prediction process by treating the parameters as random variables (see Muñoz et al. 2013 [44] for more detailed information about this approach).

Variable selection was performed beginning with all possible interaction terms, but only the best combination of variables was chosen. Such choice was based on two criteria: Deviance Information Criterion (DIC) [45] and on the cross validated logarithmic score (LCPO) measure [46]. Specifically, DIC was used as a measure for goodness-of-fit, while LCPO as a measure of the predictive quality of the models. DIC and LCPO are inversely related to the compromise between fit, parsimony and predictive quality.

All the analyses were performed using the Integrated Nested Laplace Approximation (INLA) methodology [47] and INLA package [48], in R software [24].

We used two separated approaches to assess the predictive accuracy of the selected model. Firstly, the predicted and observed values using the full dataset were compared. Secondly, a 10-fold cross validation using a random half of the dataset was performed to build the model and the remaining data to test the prediction [49].

Two statistics were calculated for both approaches: Pearson's correlation coefficient *r* and the average error (AVEerror). Pearson's correlation coefficient, *r*, measures the linear dependence between predicted and observed values. It can vary from -1 to 1, with 1 representing a perfect positive correlation between the two datasets. The AVEerror represents the mean error between observed and predicted values. The closer this statistic is to zero, the better the prediction [50].

2.4. Results

2.4.1. Bayesian models

Yellowfin tuna abundance was mainly explained by bathymetry, Chl-*a*, SST, slope, the interaction between SST and Chl-*a*, and the random spatial and temporal effects (Table 3), according to the model with the best fit (based on the lower DIC and LCPO). Distance from the coast and salinity were not relevant variables, as all models with these effects showed higher DIC and LCPO than those without them.

Table 3. Numerical summary of the posterior distribution of the fixed effects for the best model of the Yellowfin tuna. This summary contains mean, the standard deviation (SD), the median (Q0.5) and a 95% credible interval (Q0.025 - Q0.975), which is a central interval containing 95% of the probability under the posterior distribution. Chl-a = Chlorophyll-a concentration, SST = Sea Surface Temperature.

Predictor	Mean	SD	**$Q_{0.025}$**	**$Q_{0.5}$**	**$Q_{0.975}$**
Intercept	1.28	0.45	0.23	1.12	2.13
Bathymetry	-1.10	0.33	- 2.34	-0.98	-0.11
Slope	0.87	0.13	0.11	0.81	1.45
SST	0.84	0.27	0.08	0.77	1.14
Chl-a	1.42	0.22	0.33	1.40	2.54
Chl-a x SST	1.94	0.15	0.13	0.89	2.56

Yellowfin tuna showed to be more abundant in shallower waters (posterior mean = -1.10; 95% CI = [-2.34, -0.11]), according to the model. Also, higher abundance of Yellowfin tuna should be expected in warmer waters (posterior mean = 0.84; 95% CI = [0.08, 1.14]), with higher primary productivity (i.e., higher concentrations of Chl-a) (posterior mean = 1.42; 95% CI = [0.33, 2.54]) and more complex bottoms (e.g. rocky ledges). The interaction between SST and Chl-a concentration showed a positive relationship (posterior mean = 1.94; 95% CI = [0.13, 2.56]): Yellowfin tuna abundance increased in warmer waters with higher concentration of Chl-a.

Maps of the predicted abundance of Yellowfin tuna in sampled and non-sampled areas were generated for intervals of 3 years (1993-1995; 1996-1998; 1999-2001; 2002-2004; 2005-2007; 2008-2010; 2011-2013). The spatial patterns of Yellowfin tuna abundance are consistent with the model predictions, as higher abundances were predicted in shallower waters, closer to the coast where the productivity is higher and where the seabed shows some structuring (Fig 3). Predictive maps suggest a decreasing trend in the abundance of Yellowfin tuna between 1993 and 2013, but such trend showed no correlation with the ENSO events (Fig 3).

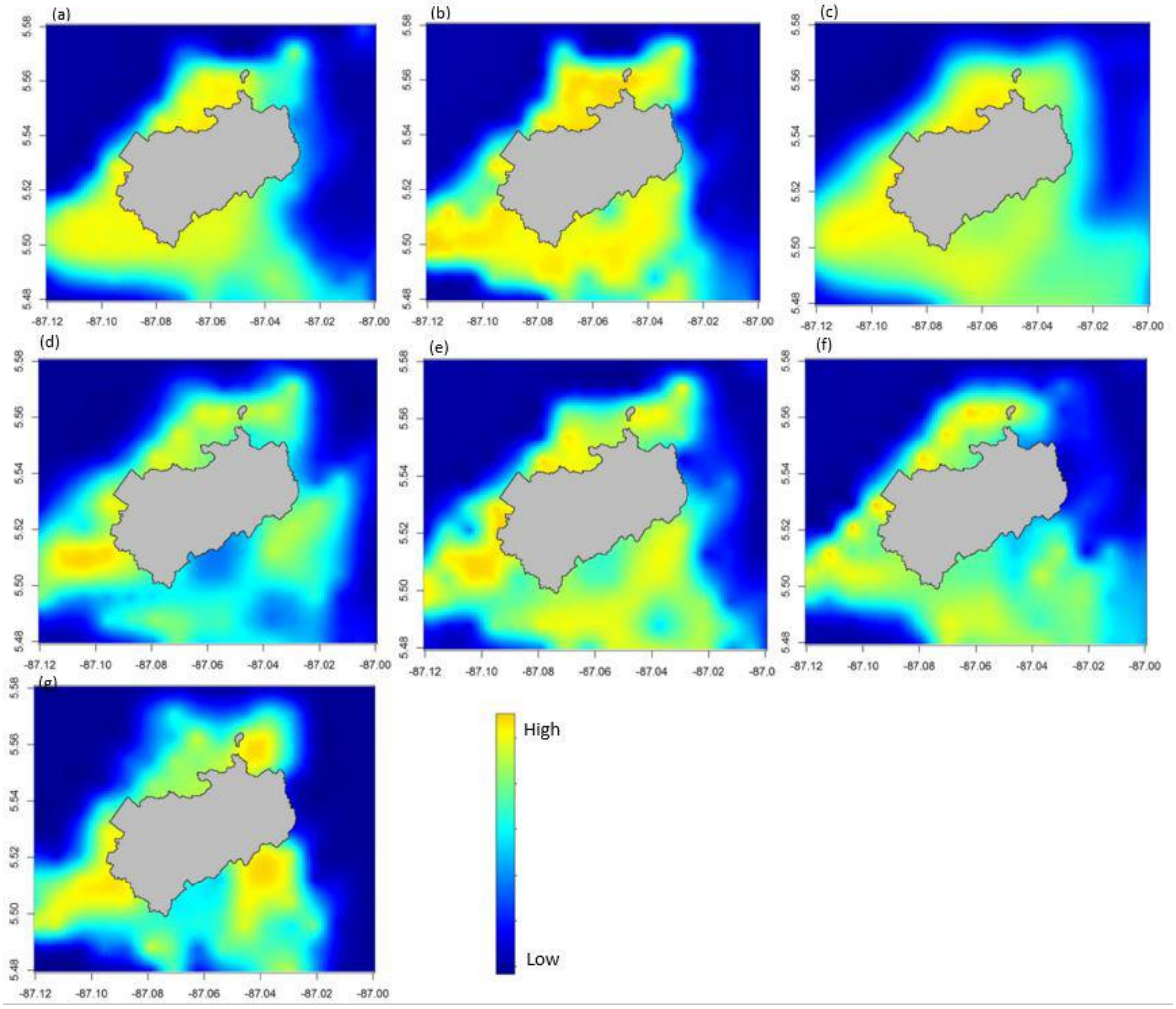


Fig. 3. Predictive maps of the abundance of the Yellowfin tuna (*Thunnus albacares*) aggregated in intervals of 3 years: (a) 1993-1995; (b) 1996-1998; (c) 1999-2001; (d) 2002-2004; (e) 2005-2007; (f) 2008-2010; (g) 2011-2013.

In addition, Pearson and Spearman's correlations (Table 4) confirmed that there was no influence of the ENSO events of the Yellowfin Tuna abundance. Indeed, both the SOI and MEI indexes were not correlated with the Yellowfin tuna abundance.

Table 4. Correlation between MEI and SOI indexes and the Yellowfin tuna abundance from 1993 to 2013.

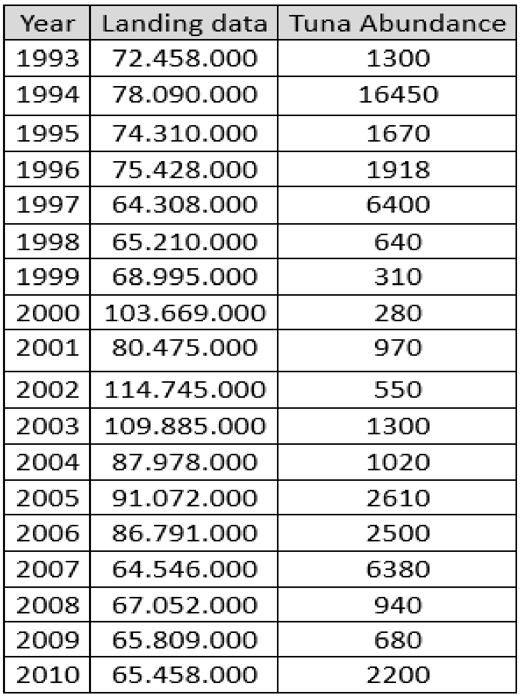
	Spearman's correlation	Pearson's correlation
MEI Index	r = -0.02, p-value = 0.65	r = 0.06, p-value = 0.43
SOI Index	r = -0.04, p-value = 0.52	r = 0.05, p-value = 0.38

The selected model presented a good fit, showed by the high values for the Pearson's correlation coefficient both for the original dataset (0.71, p-value = 0.01) and for the cross validation done with half of the dataset (0.77, p-value = 0.01). Likewise, low values for the AVEerror were achieved in both the original (AVEerror = 0.03) and in the cross validation (AVEerror = 0.02) datasets.

2.4.2. Landing data

The temporal trend of the landings of the Yellowfin tuna for the entire Costa Rica EEZ shows a clear increasing in the catches of this species from 1999 onward, followed by a stabilization at lower levels in the last years of the times series, particularly after 2007 (Table 5). On the other hand, the visual census data for Isla del Coco suggest that the number of individual Yellowfin tunas was higher in the first years of observation, reached a peak in 1997, and then decreased to its lowest level in 1998, remained at this level since then (Table 5).

Table 5. Temporal trends of landings and sightings of Yellowfin tuna. Landings (in tonnes) refer to the entire Costa Rica EEZ and refer to the period 1993 to 2010.



Year	Landing data	Tuna Abundance
1993	72.458.000	1300
1994	78.090.000	16450
1995	74.310.000	1670
1996	75.428.000	1918
1997	64.308.000	6400
1998	65.210.000	640
1999	68.995.000	310
2000	103.669.000	280
2001	80.475.000	970
2002	114.745.000	550
2003	109.885.000	1300
2004	87.978.000	1020
2005	91.072.000	2610
2006	86.791.000	2500
2007	64.546.000	6380
2008	67.052.000	940
2009	65.809.000	680
2010	65.458.000	2200

2.5. Discussion

Underwater survey censuses of the Yellowfin tuna (*Thunnus albacares*) performed along 21 years were used to improve our understanding of habitat selection by this species and its changes in distribution and abundance over time in Isla del Coco National Park. These data represent the only long-term sighting data for Yellowfin tuna, not only for Isla del Coco, but for the entire Eastern Tropical Pacific. The analyses carried out (hierarchical Bayesian approach) represent the state-of-the-art to predict species abundance, while they also account for a spatial temporal component, an important effect commonly overlooked in most studies.

The strongest predictors of the Yellowfin tuna habitats in Isla del Coco were chlorophyll and water temperature. These two factors are strongly related with ecosystems primary production, by influencing the availability of food [36, 39, 40]. This result is consistent with other studies that had already suggested that Yellowfin tuna is highly influenced by the primary production [39,51,52].

Another important factor that affects the distribution of this species is the seabed topography and structure. Isla del Coco sits atop the Coco Volcanic Cordillera, a submarine mountain offshore the southern part of Costa Rica [53,54], which apparent attracts aggregation of Yellowfin tuna [55-57]. Indeed, seamounts may act as midocean reference points that occasionally harbor increased prey densities that attract this species [58, 59].

Previous studies have observed the preference of Yellowfin tuna for shallower waters [60,61], which was confirmed here, as all predictive maps estimated higher abundances in depths between 20-80 m, and lower abundances between 90-100 m. Such findings are also in line with previous tagging studies that showed that this fish spent 85% of its time in waters close to the thermocline [61] in Isla del Coco, which happens around 50 m deep [62,63].

The predictive maps also showed that the southeast part of the island holds higher abundance of Yellowfin tuna. Since slope and bathymetry vary little around Isla del Coco [64] the preference for these areas could be due to a higher average concentration of nutrients. The south side of the island is influenced by the North Equatorial Counter Current [65, 66] and high values have been reported from that area [67], which could generate a higher productivity in the southeast.

Whereas Yellowfin tuna distribution is affected by the water temperature, probably due to its effect on productivity, it does not seem to be affected by the ENSO events. Only in the second group of years (1996-1998) there is a higher abundance that could be due to the 1997 ENSO event, as already demonstrated by Torres-Orozco et al. (2006) [68] in the Gulf of California. This could be because the study area is probably in the middle of the distribution range of this species, where climate changes do not significantly affect its distribution. Further studies with data sampled in a larger area should be done, to better understand the effects of ENSO on the entire distribution of Yellowfin tuna.

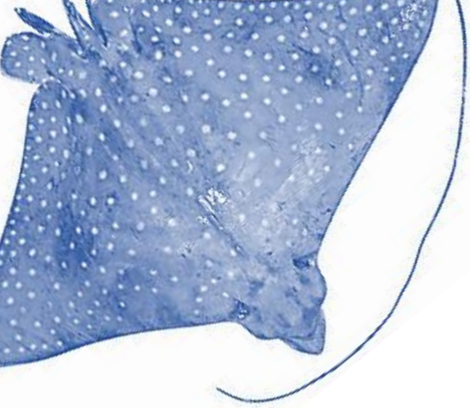
The temporal and spatial trends found in this study clearly indicate a decreasing pattern in the abundance of this species and shifts in its geographical distribution. This decrease could not be due to a possible "learning effect" of the observers. Although divers acquire more experience with time and learn to identify and count individuals better, the Bayesian analysis did not select the observer effect as possible predictor in the final model, suggesting that eventual variability in the data due to divers is low.

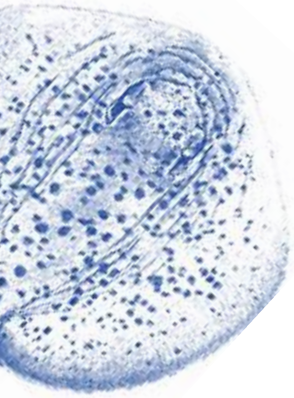
Moreover, the increasing trend of landings of this species in the 2000s in all the Costa Rica EEZ could be the direct cause of the lower sightings of this species in the Island. Isla del Coco is recognized as an example of a successful MPA and a well-known site for worldwide divers for large pelagic watching [5, 10, 69]. This fact could imply, as already suggested by White et al. (2015) [10], a problem of shifting baselines, with recreational divers failing to recognize how much of the megafauna of Isla del Coco has already been lost.

It is unclear if the current decreasing trend of the Yellowfin tuna in Isla del Coco is an indicative of an ineffective management of the MPA and/or an inducted effect of the fisheries that operate in the entire Costa Rica EEZ. Indeed, although management efforts have increased in the past decade, illegal fishing still occurs within the island’s waters [11, 70]. However, has this species has a wide distribution species, animals that get to Coco crossed waters fished by many other countries. The decrease could also be due to fishing anywhere else on the route to Coco.

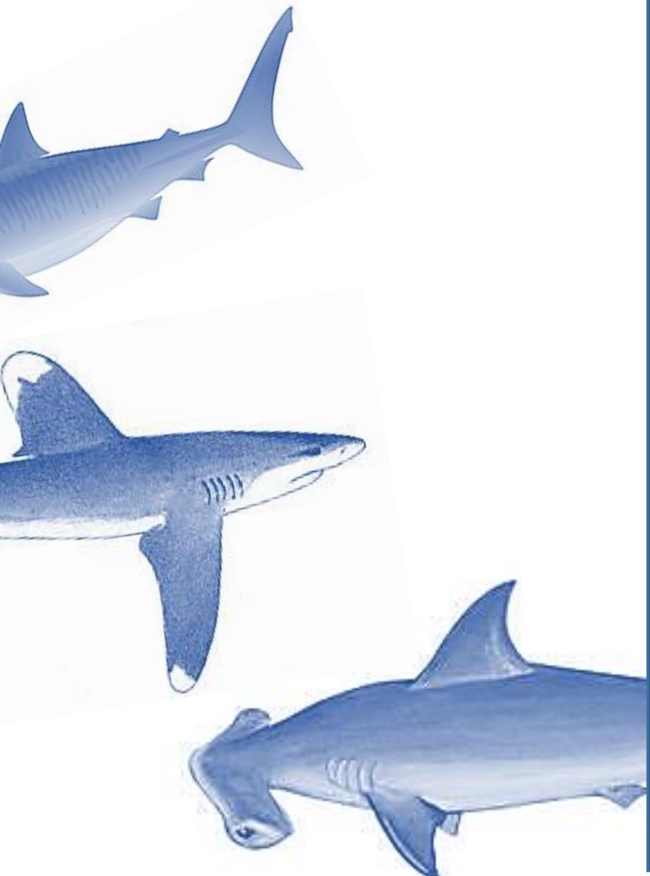
On the other hand, hot-spots of Yellowfin tuna in Isla del Coco could also be an indication of a positive effect of the MPA that has preserved this species in the waters surrounding the island [70]. A significant increase in the abundance of this species will likely be achieved only through much larger and strategic protected areas that also consider the life cycle, as this is a highly mobile pelagic species subjected to intense fishing mortality.

Further studies are needed to extend the spatial scale of the predicted distribution of this high mobility species and to understand if the possible fishing effects are directly connected with the decreasing abundance of this species. However, understanding the habitat preferences of this species using approaches as the one developed here may help design integrated programs for more efficient management of marine resources.





Chapter 3: Predictive habitat suitability models to aid the conservation of elasmobranchs in Isla del Coco National Park (Costa Rica)



Predictive habitat suitability models to aid the conservation of elasmobranchs in the Isla del Coco National Park (Costa Rica).

3.1. Abstract

Worldwide there is increasing concern for elasmobranch species given that their biological and ecological characteristics make them highly vulnerable to fishing pressure. The disappearance of these species could affect the structure and function of marine ecosystems, which would induce changes in trophic interactions at the community level. For effective conservation and management of elasmobranchs detailed knowledge of their habitat preferences is essential. Yet, there is a poor understanding of their spatial ecology. Isla del Coco National Park is an oceanic island in Pacific Costa Rica and renowned for being a sanctuary for migratory pelagic species, such as elasmobranchs. However, the abundance of many of these species has been rapidly declining over the last decades as a result of overexploitation (legal and illegal fishing). Within this context, Generalized Additive Models were performed to investigate the environmental preferences of eight elasmobranch species in Isla del Coco National Park using six predictors (i.e., sea surface temperature, salinity, chlorophyll-a concentration, bathymetry, distance from the coast and slope). Results demonstrate similar habitat preferences based on distance from the coast, slope and chlorophyll, which indicates that elasmobranchs prefer shallow waters near the island with varying degrees of slope. This study helps to identify both some of the hotspots for elasmobranchs biodiversity in Isla del Coco National Park. This approach provides an essential and relatively easy tool, such as predictive distribution maps, to increase our knowledge of marine habitats in Isla del Coco to better manage them and other offshore marine protected areas

3.2. Introduction

In marine environments apex predators play a crucial role in maintaining oceans health [1] and represent a key species within the marine system given their ability to regulate species abundance, distribution, and diversity by controlling prey densities and increasing competition [2,3]

Most elasmobranchs are predators either at or near the top of marine food chains and, thus, play an important role in marine ecosystems [2], help maintain complex ecosystems by providing food sources for scavengers [3], remove weak individuals from prey stocks [1,4], and potentially regulate the size and dynamics of their prey populations [1]. Should the abundance of elasmobranchs decrease in marine ecosystems, it could affect the structure and functions of these species and lead to changes in trophic interactions at the community level as a result of the selective removal of prey species and competitors. There is increasing concern for elasmobranch species worldwide given the late onset of their sexual maturity and their low fecundity and low natural mortality rates, which result in a low intrinsic population increase rate [5] and makes them more susceptible to population depletion as a result of anthropogenic activities, such as unsustainable fisheries, by-catch, and habitat modification [6-11].

A consequence of coupling this high vulnerability with excessive fishing pressure is that many elasmobranch species are now considered to be at a heightened risk of extinction. Currently 20% of shark species and 16% of ray species are listed as threatened (critically endangered, endangered, or vulnerable) by the International Union for Conservation of Nature (IUCN) [12]. Despite this recognition, there remains a lack of sufficient data to assess the global threat status of many elasmobranch species, with 46% of those on the IUCN Red List classified as data deficient [12].

On a regional scale, this negative trend has also been evidenced in some areas of the central-western Pacific Ocean, where recent analyses suggest that reef [13,14] and pelagic sharks [15] have declined enormously. The Pacific coast of Costa Rica is an important area for elasmobranchs as it supports a large community of these species [16]. The Isla del Coco National Park (PNIC), specifically, is among the areas in Costa Rica with the greatest abundance and richness of elasmobranchs. This oceanic island, located 500 km off the Pacific coast of Costa Rica [17, 18], is renowned for its exceptional biological value [17-19] and for being a sanctuary for migratory pelagic species, such as elasmobranchs [19].

The PNIC covers a land surface protection area of $24km^2$ [20, 18], an absolute protection marine environment of 12 nautical miles around Isla del Coco [18], and a conservation area, the Seamounts Marine Managements Area, where bottom trawling and purse seining are prohibited and longlining is regulated [22,23].

In general, comprehensive monitoring of elasmobranch populations is carried out from fisheries-dependent data or research survey data. Therefore, estimating population trends is difficult in places with insufficient regulations, no formal data collection, no fishing activities, or when there is a lack of resources to monitor population trends, as is the case in marine reserves [23,24]. This difficulty is even more pronounced when it comes to many species of reef sharks and rays that inhabit islands or remote areas with littled monitoring or management, as is the case with the PNIC [23,25]. Recent analyses suggest that reef sharks have declined enormously in both the Caribbean [26] and the central western Pacific Ocean [13,14] as well as PNIC.

Within this context, in this study we analysed the occurrence data of eight elasmobranch species, collected through underwater visual censuses between 1993 and 2013 in the PNIC and combined this with oceanographic (sea surface temperature, salinity and chlorophyll-a concentration) and topographic (depth, slope of the seabed and distance from the coast) variables using Generalized Additive Models (GAMs) to (1) understand the habitat preferences and spatial ecology of elasmobranch species and (2) identify elasmobranch hotspot areas. In addition, cluster analyses were applied to occurrence data in order to verify whether the eight species studied are in fact representative of the whole elasmobranch community in this area.

A better understanding of the temporal and spatial scales at which elasmobranch species move could provide insights on habitat use, key sites occupied, and other essential information toward effective management of these highly mobile predators in the PNIC.

3.3. Material and Methods

3.3.1. Study area

The study area is located in the eastern tropical Pacific (N 05°31´08´´, W 87°04´18´´), 500 km southwest of Costa Rica's Pacific coast [18]. The 24km^2 island is surrounded by an insular platform that covers an area of about 300km^2 and initially deepens to around 180m before dropping to several thousand meters deep [27,28]. This submerged platform consists of rocky outcrops and sandy bottoms [29,30]. The waters surrounding Isla del Coco provide an exceptional habitat for marine organisms due to the island's isolation, associated reef and seamount complexes, and its position at the confluence of several major oceanic currents [18].

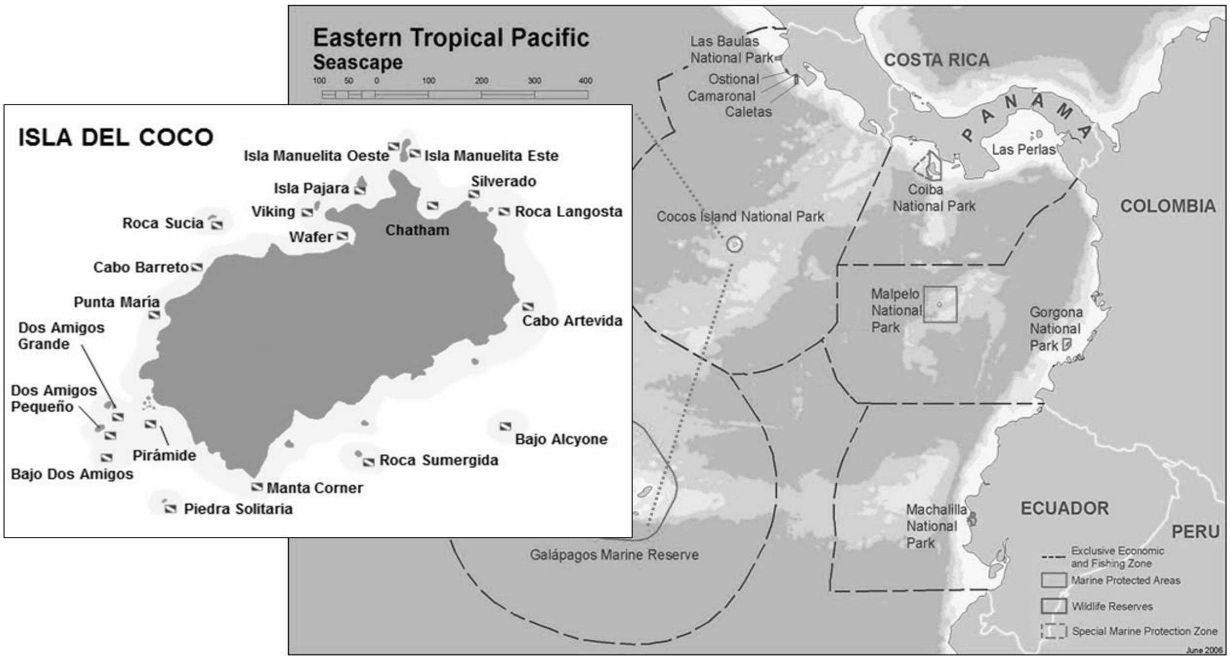


Fig 1. Map of the eastern tropical Pacific with inset of PNIC, Costa Rica and the dive locations where the underwater visual censuses were carried out (http://www.ultima-frontera.com, http://www.migramar.org).

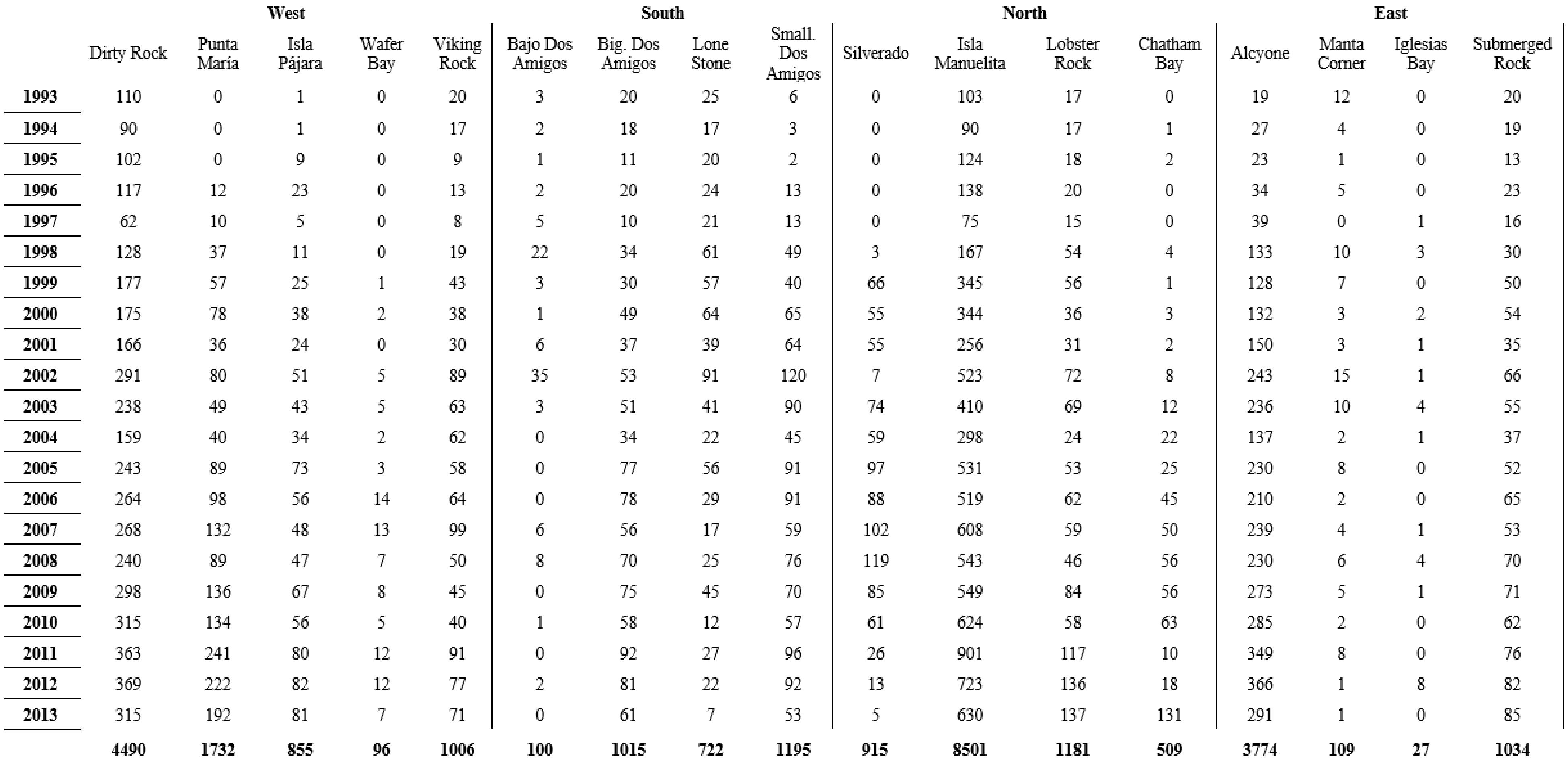
These characteristics have provided Isla del Cocos with exceptional biodiversity and are what led to it being designated a national park in Costa Rica in 1978 [18, 21]. This designation was first extended in 1984 to include the marine environment and again, in 2001, to encompass 22.2 km around the island [18, 20]. In addition, this Park was named a UNESCO World Heritage Site in 1997 and a

Ramsar site in 1998. In March 2011a marine protected area covering 9,640 km^2 surrounding Cocos, called Seamounts Marine Managements Area, was created to protect this area [18, 31].

3.3.2. Collected data

Undersea Hunter (http://undersea hunter.com/) is a privately-owned diving company that works in Isla del Cocos and has the longest underwater visual censuses (UVC) dataset for elasmobranchs in the eastern tropical Pacific [20, 32]. This dataset includes sightings information from 17 different sites around Isla del Coco between January 1993 and December 2013 (n = 21 years) (Fig.1) from a total of 27,261 immersions (Table 1). The duration of each dive averaged around 60 minutes and was led by a dive master who is able to identify the most common marine species. Dive depth ranged from 10 to 40 m depending on the site, however depth was consistent within sites. The dives were not entirely standardized as they were not scientific, however the protocols were consistent throughout the study. In addition, other studies have indicated the effectiveness of using diver-collected data to assess trends in marine megafauna [33,34].

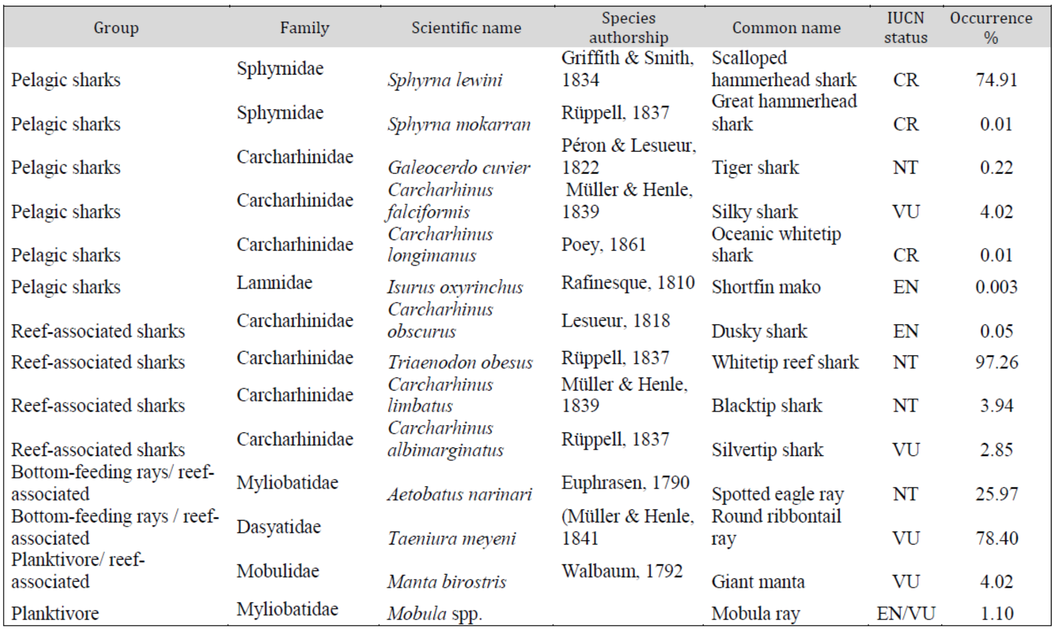
Table 1. Summary of the number of dives per year and the dive locations around the PNIC from 1993 to 2013.



	West					South				North				East			
	Dirty Rock	Punta María	Isla Pájara	Wafer Bay	Viking Rock	Bajo Dos Amigos	Big. Dos Amigos	Lone Stone	Small. Dos Amigos	Silverado	Isla Manuelita	Lobster Rock	Chatham Bay	Alcyone	Manta Corner	Iglesias Bay	Submerged Rock
1993	110	0	1	0	20	3	20	25	6	0	103	17	0	19	12	0	20
1994	90	0	1	0	17	2	18	17	3	0	90	17	1	27	4	0	19
1995	102	0	9	0	9	1	11	20	2	0	124	18	2	23	1	0	13
1996	117	12	23	0	13	2	20	24	13	0	138	20	0	34	5	0	23
1997	62	10	5	0	8	5	10	21	13	0	75	15	0	39	0	1	16
1998	128	37	11	0	19	22	34	61	49	3	167	54	4	133	10	3	30
1999	177	57	25	1	43	3	30	57	40	66	345	56	1	128	7	0	50
2000	175	78	38	2	38	1	49	64	65	55	344	36	3	132	3	2	54
2001	166	36	24	0	30	6	37	39	64	55	256	31	2	150	3	1	35
2002	291	80	51	5	89	35	53	91	120	7	523	72	8	243	15	1	66
2003	238	49	43	5	63	3	51	41	90	74	410	69	12	236	10	4	55
2004	159	40	34	2	62	0	34	22	45	59	298	24	22	137	2	1	37
2005	243	89	73	3	58	0	77	56	91	97	531	53	25	230	8	0	52
2006	264	98	56	14	64	0	78	29	91	88	519	62	45	210	2	0	65
2007	268	132	48	13	99	6	56	17	59	102	608	59	50	239	4	1	53
2008	240	89	47	7	50	8	70	25	76	119	543	46	56	230	6	4	70
2009	298	136	67	8	45	0	75	45	70	85	549	84	56	273	5	1	71
2010	315	134	56	5	40	1	58	12	57	61	624	58	63	285	2	0	62
2011	363	241	80	12	91	0	92	27	96	26	901	117	10	349	8	0	76
2012	369	222	82	12	77	2	81	22	92	13	723	136	18	366	1	8	82
2013	315	192	81	7	71	0	61	7	53	5	630	137	131	291	1	0	85
	4490	**1732**	**855**	**96**	**1006**	**100**	**1015**	**722**	**1195**	**915**	**8501**	**1181**	**509**	**3774**	**109**	**27**	**1034**

We classified species into four categories: (1) pelagic sharks, including *Sphyrna lewini* (scalloped hammerhead), *Sphyrna mokarran* (Great hammerhead), *Galeocerdo cuvier* (Tiger shark), *Carcharhinus falciformis* (Silky shark), *Carcharhinus longimanus* (Oceanic whitetip shark) and *Isurus oxyrinchus* (Shortfin mako); (2) reef-associated sharks, including *Carcharhinus obscurus* (Dusky shark), *Triaenodon obesus* (Whitetip reef shark), *Carcharhinus limbatus* (Blacktip shark) and *Carcharhinus albimarginatus* (Silvertip sharks), (3) bottom feeding rays, including *Aetobatus narinari* (Spotted eagle ray), and *Taeniura meyeni* (Marble rays); and (4) planktivores, including *Manta birostris* (Manta ray) and *Mobula* spp. (Mobula) (Table 2). These species are part of the PNIC elasmobranch community, whose taxonomic breadth spans across seven families and possess an array of life history traits [19] (Table 2). The species *S. mokarran, G. cuvier, C. longimanus, C. obscurus, I. oxyrinchus* and *Mobula* spp. have very low occurrences (Table 2) and, therefore, it was not possible to develop habitat sensitivity maps for them. However, they have been included in the cluster analysis (Fig. 3).

Table 2. Elasmobranch species observed during dives around the PNIC between 1993 and 2013. IUCN Red List Categories: EN "Endangered, NT "Near Threatened", VU "Vulnerable" and CR "Critically Endangered". Occurrence describes the number of dives in which the species was sighted (expressed as a percentage).



Group	Family	Scientific name	Species authorship	Common name	IUCN status	Occurrence %
Pelagic sharks	Sphyrnidae	*Sphyrna lewini*	Griffith & Smith, 1834	Scalloped hammerhead shark	CR	74.91
Pelagic sharks	Sphyrnidae	*Sphyrna mokarran*	Rüppell, 1837	Great hammerhead shark	CR	0.01
Pelagic sharks	Carcharhinidae	*Galeocerdo cuvier*	Péron & Lesueur, 1822	Tiger shark	NT	0.22
Pelagic sharks	Carcharhinidae	*Carcharhinus falciformis*	Müller & Henle, 1839	Silky shark	VU	4.02
Pelagic sharks	Carcharhinidae	*Carcharhinus longimanus*	Poey, 1861	Oceanic whitetip shark	CR	0.01
Pelagic sharks	Lamnidae	*Isurus oxyrinchus*	Rafinesque, 1810	Shortfin mako	EN	0.003
Reef-associated sharks	Carcharhinidae	*Carcharhinus obscurus*	Lesueur, 1818	Dusky shark	EN	0.05
Reef-associated sharks	Carcharhinidae	*Triaenodon obesus*	Rüppell, 1837	Whitetip reef shark	NT	97.26
Reef-associated sharks	Carcharhinidae	*Carcharhinus limbatus*	Müller & Henle, 1839	Blacktip shark	NT	3.94
Reef-associated sharks	Carcharhinidae	*Carcharhinus albimarginatus*	Rüppell, 1837	Silvertip shark	VU	2.85
Bottom-feeding rays/ reef-associated	Myliobatidae	*Aetobatus narinari*	Euphrasen, 1790	Spotted eagle ray	NT	25.97
Bottom-feeding rays / reef-associated	Dasyatidae	*Taeniura meyeni*	(Müller & Henle, 1841	Round ribbontail ray	VU	78.40
Planktivore/ reef-associated	Mobulidae	*Manta birostris*	Walbaum, 1792	Giant manta	VU	4.02
Planktivore	Myliobatidae	*Mobula* spp.		Mobula ray	EN/VU	1.10

3.3.3. Environmental variables

Six environmental variables were considered as potential predictors of elasmobranch occurrence and were selected for being known to influence species distribution. These included three bathymetric features: distance from the coast (in meters), slope (in %) and bathymetry (in meters), and three oceanographic variables: chlorophyll-a concentration (Chl-a, mg m^{-3}), sea surface salinity (SSS, in PSU) and sea surface temperature (SST, in ºC).

Chl-a concentration was included in the analysis as a possible index of primary production of an ecosystem [37]. Indeed, several studies have shown that primary production is an important factor that drives elasmobranch abundance and distribution [38]. SSS and SST are strongly related to marine system productivity as they can affect nutrient availability, metabolic rates, and water stratification [39,40]. SST and Chl-a variables were extracted from different sensors as nightly monthly means and aggregated into yearly maps using the Spatial Analysis tool of ArcGIS 10 (Table S1 Appendix).

As no exhaustive and validated SSS time series was available, the monthly SSS climatology was downloaded from the World Ocean Database 2013 (WOA13) (Table S1 Appendix).

Distance from the coast and bathymetry were considered for analysis as they are among the main factors that control species distribution and have previously been identified as predictors to determine spatial patterns of many elasmobranchs [41,42].

Slope is an index of seabed morphology and has previously been used as a predictor of species distribution and suitable habitats [43-46]. Low slope values correspond to a flat oceanic bottom (or areas of sediment deposition), whereas higher values indicate potential rocky ledges. Slope has previously been used as predictor of reef-associated species distribution [44].

All bathymetric features were derived from the MARSPEC database [47]. MARSPEC is a world ocean dataset that was developed for marine spatial ecology and has a spatial resolution of 0.01 x 0.01 degrees [48].

All environmental variables were explored for collinearity, outliers, and missing data before being used in the analysis and modelling [49]. These variables were aggregated with a spatial resolution of 0.01 x 0.01. To facilitate observation and interpretation, the explanatory variables were standardized (difference from the mean divided by the corresponding standard deviation).

3.3.4. Cluster Analysis

To verify whether the eight most sighted species were truly representative of the whole elasmobranch community, a Cluster Analysis (CA) was carried out. The Euclidean distance was used as a similarity measure and the Ward's method as the clustering algorithm [36]. The Ward's method uses a variance analysis to evaluate the distances between clusters and attempts to minimize the total within-cluster variance [50] and compute each cluster uncertainty by obtaining their Approximate Unbiased p-values (AU p-values). A matrix with the 27,261 dives was developed to fit the CA considering the occurrence of the eleven elasmobranch studied species, CAs were fitted using the "pvclust" package [51] of the R software [52].

If results show a high degree of similarity between the species assemblage of the different dives, the sensitive habitats identified for the eleven studied species are assumed to be shared by the remaining elasmobranch species. Consequently, the conservation of these habitats would go a long way to protect the entire community of elasmobranchs in this area [39, 53].

3.3.5. Statistical analysis

Generalized additive models (GAM) [54,55] were fitted to identify the environmental characteristics associated to elasmobranch distributions. GAMs are extensions of generalized linear models (GLMs) and use smooth functions to replace linear and other parametric terms. These models were chosen over generalized linear models as they are capable of capturing non-linear relationships by fitting smoothing functions to predictor variables [56- 58].

The presence/absence of each of the eight selected species was considered to be the dependent variable. The degrees of freedom of the smooth functions were restricted to four for each explanatory variable to avoid additional over-fitting.

GAMs were fitted using a binomial family with a logistic link function. A forward step-wise variable selection procedure, which consists of building the null model (only the overall mean is used as a predictor variable) and then adding a new covariate to check its contribution to the model, was applied to establish the best models. Finally, the best model for each species was selected based on the lowest Akaike Information Criterion (AIC), the unbiased risk estimator (UBRE) [59], the highest explained deviance, and by retaining only significant variables that did not equal zero at any point throughout the predictor range. GAMs were fitted using the "*mgcv*" package [60] of the R software [52].

3.3.6. Model evaluation

For each species the occurrence dataset was randomly divided into two subsets: one with 80% of the data used to fit the model (training dataset), and the other with the remaining 20% of the data to evaluate the model (validation dataset). The training dataset was used to model the relationship between occurrence data and environmental variables, whereas the validation dataset was used to assess the quality of predictions. For each chosen model for each species, the validation process was repeated five times and the results were averaged across the different randomized subsets.

The prediction evaluation of the binomial models was performed using the area under the receiver-operating curve (AUC) [61,62], specificity, sensitivity and the True Skill Statistic (TSS) [63]. AUC measures the ability of a model to discriminate between sites where a species is absent and where it is present. The AUC has been widely used in species distribution models [62]. The AUC ranges from 0 to 1. A value of 1 indicates that the model can distinguish between occupied and unoccupied sites; values less than 0.5 indicate that the model does not work better than a random model; values between 0.7 and 0.9 indicate very good discrimination; and values > 0.9 are excellent. The AUC is tabulated through the confusion matrix, which indicates false negatives (FN), false positives (FP), true positives (TP), and true negatives (TN). Two types of prediction errors are generally assumed: FN leads to under-prediction and FP leads to over-prediction. The confusion matrix is used to calculate the criteria of sensitivity, specificity and TSS. Specificity is the proportion of TN that is correctly predicted, and sensitivity is the proportion of TP that is correctly predicted. Specificity reflects a model's ability to predict an absence when a species does not occur at a location, and sensitivity reflects a model's ability to predict a presence when a species does in fact occur at a given location. TSS is the sum of the rates correctly classified as presences (TP) and absences (TN). This represents a balance between model maximizing sensitivity and specificity. Its range is -1 to 1, where a high value is optimal. The model validation was performed using the "*PresenceAbsence*" [64] R-package [52].

3.4. Results

3.4.1. Presence of elasmobranchs

A total of 27,261 dives were observed over a 21-year period (1993-2013).

The highest number of occurrences was recorded for *T. obesus* with 97.26%, followed by *T. meyeni* with 78.41%, and *S. lewini* with 74.91% (Table 2). *Sphyrna mokarran, G. cuvier, C. longimanus, I. oxyrinchus, C. obscurus,* and *Mobula spp*. had occurrences of less than 1%. (Table 2).

3.4.2. Cluster Analysis

The dendrogram of similarity for the individuals observed during the dives shows three different clusters of elasmobranchs (Fig. 2). *Sphyrna lewini* and *T. obesus* form two separate groups, whereas the other species are all included in a single group. The latter group includes twelve of the fourteen elasmobranch species observed in the study area (Fig. 3). Consequently, conserving the identified habitats would go a long way to protecting the entire elasmobranch community in this area.

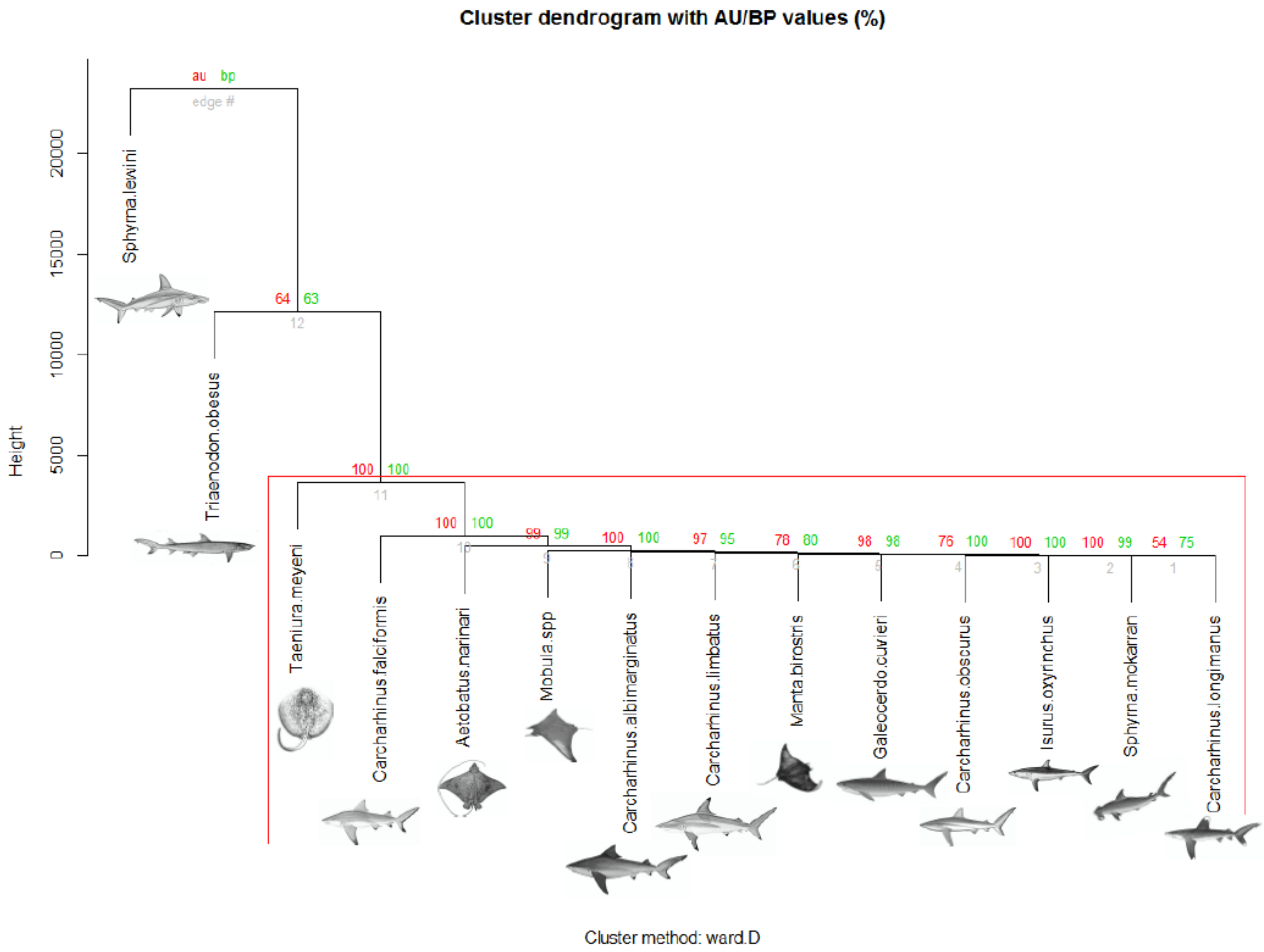


Fig. 2. Cluster Analysis (CA) dendrogram of the observed elasmobranch species during dives in Isla del Coco National Park. AU: approximately unbiased p-values. BP: bootstrap probability.

3.4.3. Environmental factors relevant to elasmobranch habitat selection

Among the six predictor variables, bathymetry and distance to coast were highly correlated (Pearson's correlation, r > 0.68), as were SST and SSS (Pearson's correlation, r > 0.7) (Table S2 Appendix). As a result, these variables were tested separately in the GAMs and only the one with the highest total explained variance was included in the final models.

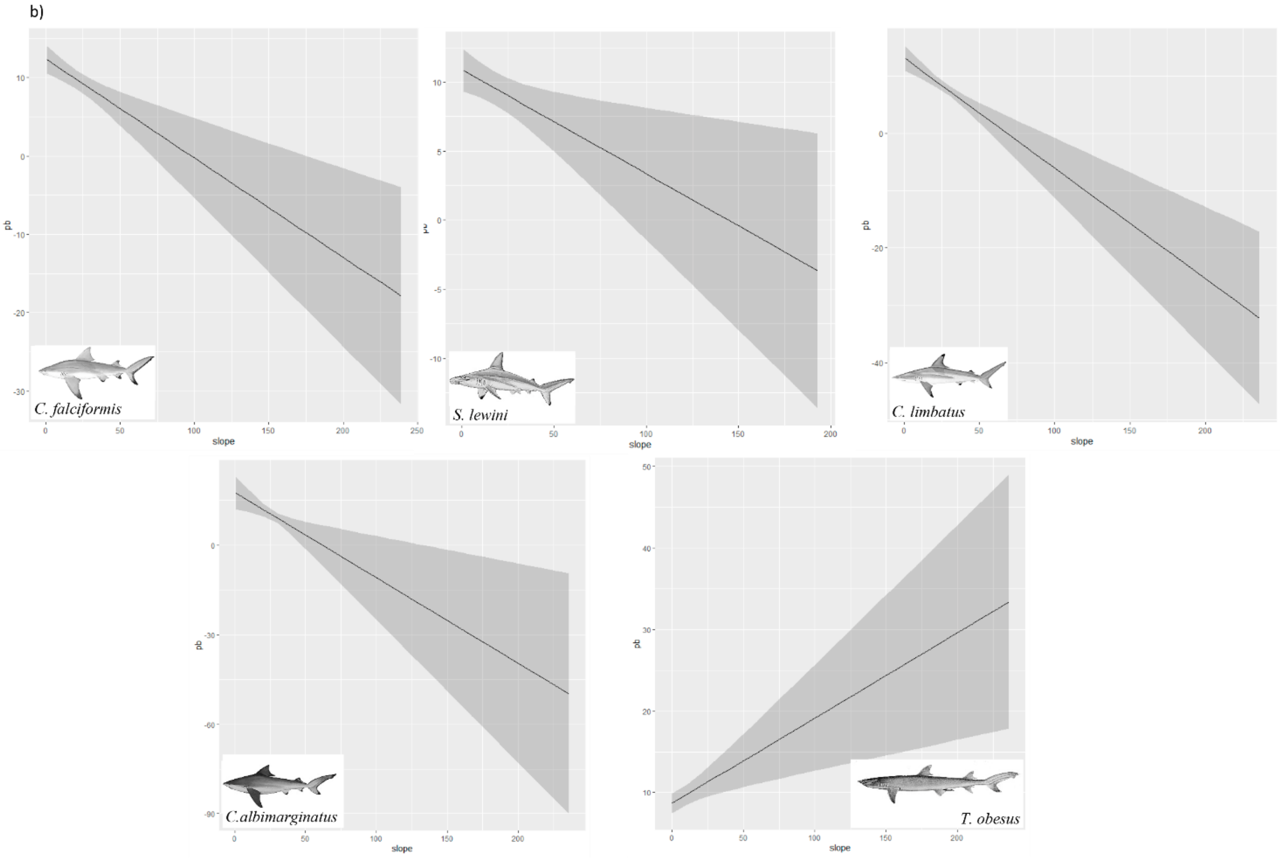
The variance inflation factor (VIF) values were between 1.9 and 2.4. and, thus were considered to be an indication of the absence of multicollinearity among the explanatory variables (Table S2 Appendix).

Distance to coast was the main significant environmental predictor for all species, except for T. *obesus* (Table 3). Bathymetry and SSS only influenced habitat suitability for *T. obesus* (Table 3). The slope was also a relevant predictor for most species, with the exceptions of *A. narinari*, *T. meyeni,* and *M. birostris* (Table 3). SST was not significant in any model (Table 3). Finally, Chl-a was found to affect the suitability of the habitat for the ray and manta groups (i.e., *A. narinari, T. meyeni*, and *M. birostris*) (Table 3).

Table 3. Selected models for the eight elasmobranchs species using Generalized Additive Models (GAM). Predictors include sea surface temperature (SST), sea surface salinity (SSS), bathymetry (bath), slope, chlorophyll (Chl-a) and distance to coast (dist). Only the best selected models are shown (variables included in model are shaded in grey). AIC: Akaike's Information Criteria, UBRE: unbiased risk estimator, and Dev: percentage of total deviance explained. Model predictions were evaluated by AUC: area under the receiver-operating curve, SENS: model sensitivity; SPEC: model specificity and TSS: True Skill Statistic.

Scientific name	**Model selection**									**Model evaluation**			
	SST	SSS	bath	slope	Chl-a	dist	AIC	UBRE	Dev (%)	AUC	SENS	SPEC	TSS
S. lewini				▨		▨	148.52	-0.99	89.20%	0.98	1	0.93	0.93
C. falciformis				▨		▨	146.70	-1.00	89.30%	0.98	1	0.93	0.93
T. obesus		▨	▨	▨			144.94	-0.99	89.90%	0.94	1	0.87	0.87
C. limbatus				▨		▨	158.54	-0.99	88.40%	0.95	1	0.92	0.92
C.albimarginatus				▨		▨	83.71	-1.00	94.10%	0.98	1	0.93	0.93
A. narinari					▨	▨	210.63	-0.99	84.60%	0.98	1	0.97	0.97
T.meyeni					▨	▨	135.99	-0.99	90.30%	0.93	1	0.88	0.88
M. birostris					▨	▨	126.51	-1.00	91%	0.97	1	0.92	0.92

The functional responses of the relationships between environmental variables and the presence of species are presented in Fig. 3. Distance from the coast was one of the most relevant predictors for most species (Table 3). Considering all species, the relationship between the probability of occurrence and the distance to coast indicates that the occurrence of elasmobranchs decreases in areas far from the coast (Fig. 3a). The variable slope showed a negative linear relationship with the probability of occurrence of S. *lewini*, *C. falciformis*, *C. albimarginatus* and *C. limbatus*, and a positive relationship with *T. obesus*, which means that the latter species had a preference for seabeds with a higher slope (Fig. 3b). For *T. meyeni, A. narinari* and *M. birostris*, the GAMs suggested a negative relationship with Chl-a concentration, which means that these species had a preference for waters with lower productivity, with an optimum of 0.17 *mg.m* -3 (Fig. 3c). Furthermore, *T. obesus* exhibited a negative trend with SSS and bathymetry, which suggests that higher occurrences were found in less saline and shallower waters (Fig. 3d,e).



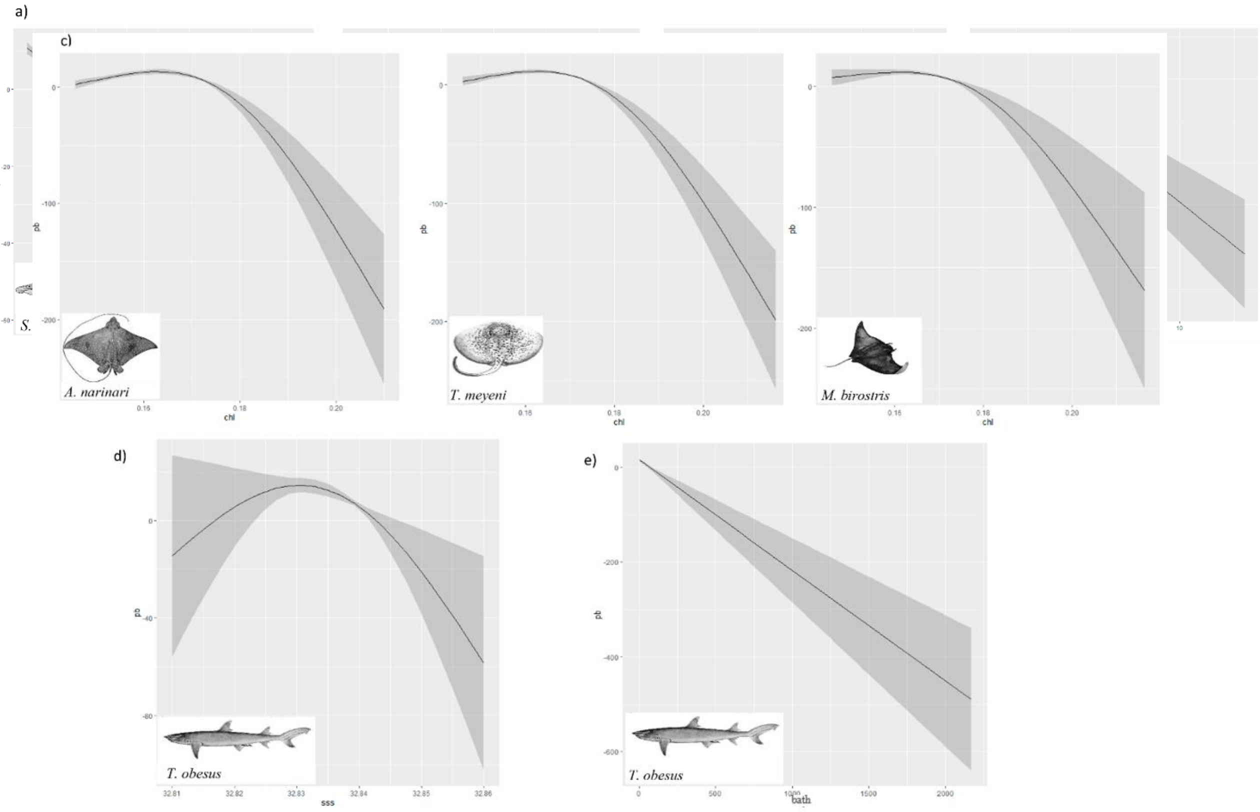


Fig. 3. GAM partial plots for the best binomial models for the studied species. Representation of the probability of occurrence of the species in the model in relation to the independent variable with the explanatory variables. Representation of species in relation to a) distance from the coast, b) slope, c) chlorophyll-a, d) salinity, and e) bathymetry. The solid line in each graph is the estimated smooth function (indicated on the y-axis label) and the dashed lines represent the approximate 95% confidence intervals around the response curve. The probability of occurrence of the species is represented on the Y-axis (logit scale) and the ranges of the environmental variables are represented on the x-axis as dist: distance from the coast (km); slope (%); Chl-a: chlorophyll-a. (mgm^{-3}); SSS= sea surface salinity; bath: bathymetry (m).

3.4.4. Model evaluation and calibration

Table 3 shows the prediction performance statistics of the final models. All models indicate excellent degrees of discrimination between the sites where a species was absent and where it was present, as indicated by AUC values greater than 0.93. High specificity and sensitivity values (> 0.93) indicate a high capacity of the model to correctly adjust true positive and negative predictions. The models have a good degree of similarity between species occurrence and evidence available (TSS values are between 0.83 and 0.93).

3.4.5. Mapping model predictions

Figure 4 presents the prediction maps of the eight most occurring elasmobranch species (*S. lewini, T. obesus*, *C. limbatus, T. meyeni*, *C. albimarginatus*, *A. narinari, C. falciformis* and *M. birostris*). Predictive maps revealed similar distribution patterns among different species in response to environmental variables. All species showed a preference for the shallow waters surrounding the Isla del Coco (Fig. 4). These areas also have low slope values that are probably characterized by rough sediments. *Taeniura meyeni* and *C. limbatus* had broader distributions in the south of Isla del Coco. *T. obesus*, the species with the highest presence (Table 3), showed a preference for shallow waters like the other species, and it also showed a preference for coastal areas with higher slopes (Fig. 4), thereby expanding its presence to the submarine mountains located in the northeast part of Isla del Coco.”

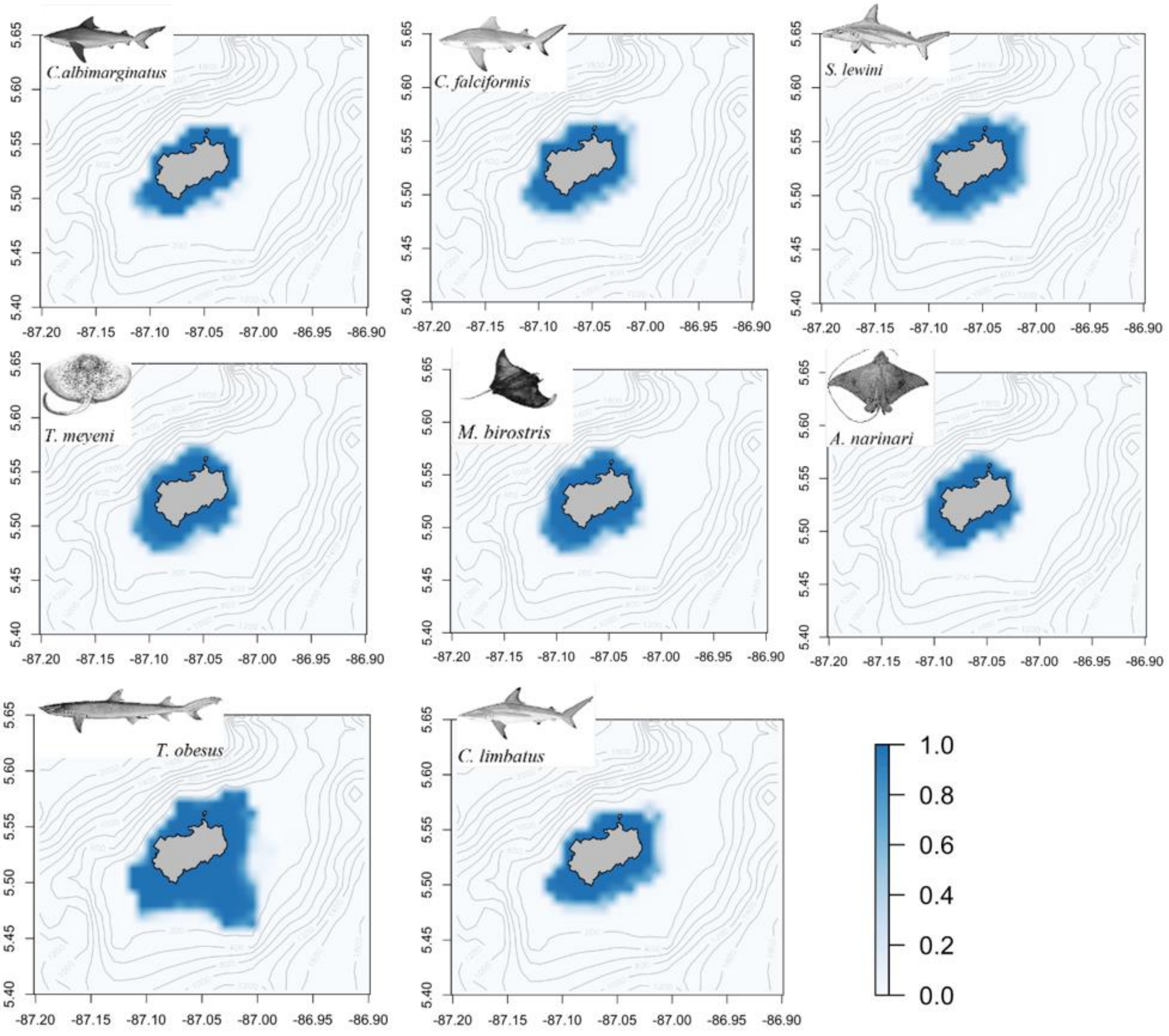


Fig. 4. Predictive maps of the presence of *C. albimarginatus, C. falciformis, S. lewini, T. meyeni, M. birostris, A. narinari, T. Obesus, and C. limbatus,* in the PNIC between 1993 and 2013.

3.5. Discussion

Underwater surveys of fourteen species, carried out over a 21 year period, were used to improve our understanding of the habitat selection and distribution of these species in the PNIC. These data represent both the only long-term sightings data for elasmobranchs in the PNIC and also in the entire eastern tropical Pacific [32,33].

CA and GAM analyses were carried out. CAs were carried out to verify whether the eight most sighted species were truly representative of the entire elasmobranch community. GAMs were carried out to assess the influence of the covariates on the presence/absence of species and to predict the probability of occurrence in non-sampled areas.

With the available data, the main predictors of elasmobranch habitats in the PNIC were found to be distance to coast and slope. The predictors chl-a and SSS revealed species-specific relationships, whereas other environmental factors did not have a consistent effect across species.

In general, considering the entire study area, the studied species showed a preference for shallower waters near the island with lower slopes. The elasmobranch species from the PNIC showed similar optimum depths, which may indicate a certain fine-tuned bathymetric aggregation. Habitat overlap does not necessarily imply competition, except when resources are in short supply. Otherwise, on rich shelf bottoms species that are spatially segregated are not driven to differentiate their diets and may easily converge to use resources in overlapping areas [39].

Overall, the greater presence of elasmobranchs in the shallower zones can be attributed to greater environmental variability in these zones, as suggested by Stevens (1989) [65]. This environmental variability favours species richness as a result of all the processes that occur in the bathymetric gradient (incidence and quantity of light, currents, thermoclines, upwelling, etc.) [66-67].

Predictive maps confirmed a congregation of species in the coastal zones that had previously been observed for some of the species in this area, such as *S. lewini, T. obesus, Mobula spp, M. birostris, G. cuvier,* and *C. limbatus*, [19,68], and which is similar to other regions of the Pacific [69,70]. For example, in the Galápagos Marine Reserve elasmobranchs are distributed near the coasts of the Floreana Islands [71]. The same pattern has been observed in other areas of the world, such as the Balearic Islands (western Mediterranean) for demersal sharks [72,73], the north-eastern Pacific Ocean for pelagic species [69], and the archipelago of Hawaii, Johnston Atoll and Cross Seamount for benthic species [74].

In addition to distance from the coast, for the habitat preference models for *A. narinari, T. meyeni* and *M. birostris* were also influenced by chlorophyll-a. The probability of presence of these three species was higher where Chl-a concentration values were lower, with an optimum of 0.18 mg-m3. Overall, high concentrations of Chl-a can affect water transparency, thereby increasing the difficulty for these species to find prey. Moreover, these Chl-a values can be found in the most important upwelling areas of the eastern Pacific Ocean, such as the Costa Rica Dome [75]. This result points to a possible preference among these species for cyclonic eddies, upwelling systems, shallow mixed layers or cold sides of thermal fronts [76].

Triaenodon obesus was the species with the highest occurrence in the PNIC. This high incidence was also documented by Zanella et al., (2012) [77]. Its distribution trend was mainly related to bathymetry and slope. The predictive map indicated that is has a wider depth range (up to 40 meters) than the rest of the elasmobranchs, and is concentrated around the Isla del Coco and extends to the area of the seamounts. *Triaenodon obesus* is the only shark in the Carcharhinidae family that is benthic and coastal; two factors associated with a limited dispersion range [78,79]. The dispersion range obtained in our study corroborates the results of Nelson and Johnson (1980) [79], who studied *T. obesus* in Rangiroa, French Polynesia, and found that the species is more abundant in coral reefs ranging between 10 and 30 m deep, in areas highly influenced by high slopes, and in areas with low bathymetry. In addition, Randall (1977) [80], points out that the shark *T. obesus* is generally found in very clear waters ranging between 8 and 40 m deep in Madagascar. Sphyrna lewini spends the first part of its life in coastal waters (breeding grounds), while adults migrate out to sea, returning to protected breeding habitats to mate and breed. The coastal waters of Isla del Coco such as Wafer Bay are a breeding and breeding ground for Sphyrna lewini, where both adults and juveniles can be found [81].

Salinity was another relevant variable for the distribution of *T. obesus,* which showed a preference for waters with lower salinity concentrations. This finding can be indirectly related to the feeding habits of this species, who feed upon crustaceans which inhabit preferably brackish and less saline waters [80].

Overall, the PNIC seamounts, islets and bays represent essential habitats (foraging, resting, cleaning, mating areas) for the various shark species studied [83-86]. The distribution maps obtained indicate a preference for areas near the coast that have these characteristics. [30].

Although the present study was limited to eight species, the elasmobranch similarity dendrogram showed that 12 of the 14 elasmobranch species observed in the PNIC frequent the same areas. These results indicate that the sensitive habitats identified for the eight studied species are shared by the other less frequently observed elasmobranchs.

Finally, we do not exclude the possibility that these distribution patterns could be marginally influenced by the limitations in the sampling data (since the dives carried out in areas near the coast generally reached a maximum depth of 35 m). This is because the deeper water areas further from the coast are generally difficult to visit.

3.6. Conclusions

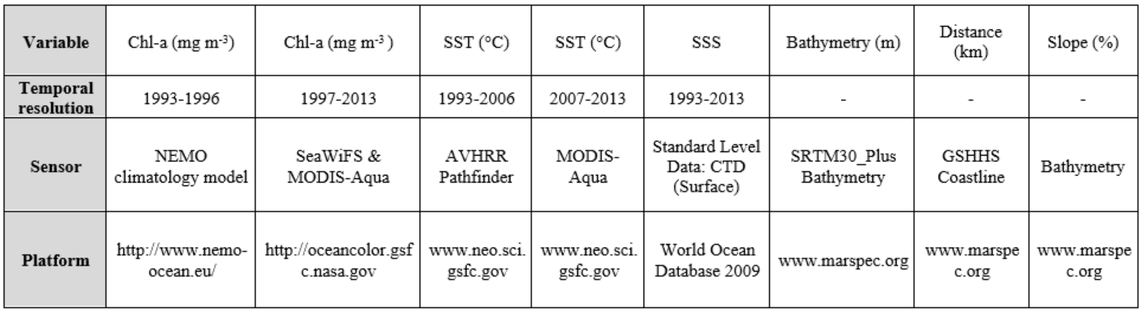
This study improves our understanding of the habitat preferences and hotspot distributions of elasmobranchs in the PNIC in an effort to contribute toward their conservation. Environmental factors, distance to coast, slope and chlorophyll-a, were found to be the main variables influencing elasmobranch habitat suitability.

Mapping sensitive habitats of vulnerable species within a region for conservation planning requires the highest level of precision. In the models obtained, the evaluation criteria demonstrated good predictive performance and advantages in terms of ecological interpretability.

Identifying and protecting critical habitats (for threatened species and community diversity) is one of the main uses of habitat suitability models for conservation purposes [87]. Preserving these habitats can contribute to protecting most species in the elasmobranch community in this area.

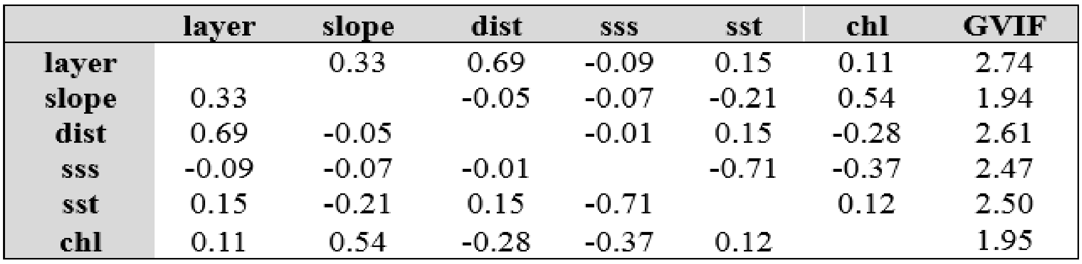
3.7. Supplementary material

Table S1 Appendix: Predictores variables used fro modeling the elasmobranch occurrence in the Isla del Coco. SST = Sea Surface Temperature, SSS = Sea Surface Salinity, Chl-a = Chlorophyll-a.

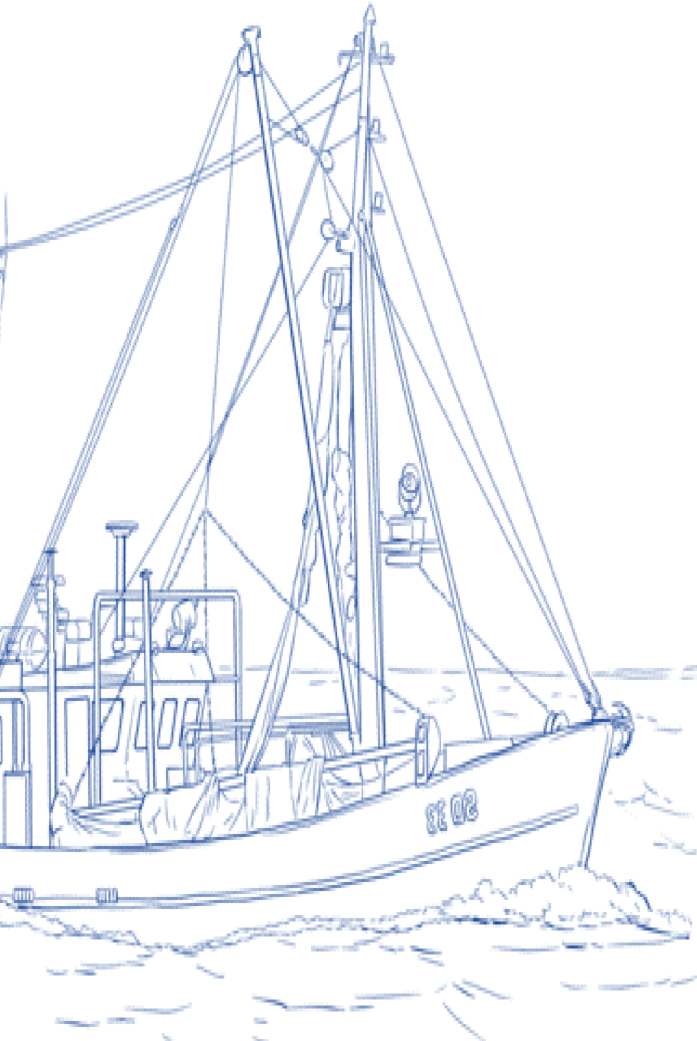


Variable	Chl-a (mg m^{-3})	Chl-a (mg m^{-3})	SST (°C)	SST (°C)	SSS	Bathymetry (m)	Distance (km)	Slope (%)
Temporal resolution	1993-1996	1997-2013	1993-2006	2007-2013	1993-2013	-	-	-
Sensor	NEMO climatology model	SeaWiFS & MODIS-Aqua	AVHRR Pathfinder	MODIS-Aqua	Standard Level Data: CTD (Surface)	SRTM30_Plus Bathymetry	GSHHS Coastline	Bathymetry
Platform	http://www.nemo-ocean.eu/	http://oceancolor.gsfc.nasa.gov	www.neo.sci.gsfc.gov	www.neo.sci.gsfc.gov	World Ocean Database 2009	www.marspec.org	www.marspec.org	www.marspec.org

Table S2 Appendix: Correlation matrix of the environmental variables included in the model.



	layer	**slope**	**dist**	**sss**	**sst**	**chl**	**GVIF**
layer		0.33	0.69	-0.09	0.15	0.11	2.74
slope	0.33		-0.05	-0.07	-0.21	0.54	1.94
dist	0.69	-0.05		-0.01	0.15	-0.28	2.61
sss	-0.09	-0.07	-0.01		-0.71	-0.37	2.47
sst	0.15	-0.21	0.15	-0.71		0.12	2.50
chl	0.11	0.54	-0.28	-0.37	0.12		1.95



Chapter 4: Illegal fishing in Isla del Coco National Park: spatial-temporal distribution and the economic trade-offs.

Illegal fishing in Isla del Coco National Park: spatial-temporal distribution and the economic trade-offs

4.1. Abstract

The Isla del Coco National Park, located on the Pacific coast of Costa Rica, is rich in biodiversity and has a high concentration of pelagic species. This high marine biodiversity makes the Isla del Coco National Park (PNIC) a very attractive place for illegal fishers. We analyzed a dataset covering 8 years (2003-2010) of patrol records from PNIC with the aim of determining, a) the spatial-temporal distribution of illegal fishing, b) other areas that could be prone to illegal fishing but are currently undetected, c) the most profitable areas for this activity and d) the economic trade-offs of this illegal activity in relation to potential gains and the costs. Residuals Autocovariate Generalized Additive Models (RAC-GAMs) were used to model the illegal fishing activity's spatial distribution in relation to topographic, biological and temporal (quarter of the year) variables. The final RAC-GAM showed that bathymetry, distance from the coast, slope of the seabed, and yellowfin tuna and silky shark abundance were the most important predictors of this activity. Predictive maps suggest a major trend in the abundance of illegal fishing between the second and third quarters of the year in waters surrounding a seamount within the Park. Maps of the most profitable areas highlighted a specific risk location that should be intensively monitored. Overall, the potential gains from this activity outweigh the potential costs of being caught. Our findings provide useful information that can be used to optimize enforcement, deter illegal fishing and, consequently, increasing the conservation of the protected species.

4.2. Introduction

Historically, a variety of names have been used to define Marine Protected Areas (MPAs) (e.g., marine reserves, sanctuaries, parks, etc.). Several reasons have been used to promote their creation, each allowing for different levels of human access [1,2]. However, to date most MPAs are not protecting seamounts, high seas and offshore archipelagos, while anthropogenic impacts and non-sustainable use of marine resources have been increasingly affecting these areas [3]. Additionally, although some of the offshore MPAs include pelagic environments, they present several common issues. In most cases these areas are not totally adequate for the conservation of pelagic species as they do not fully match the species home ranges that are highly variable in space and time [4]. Moreover, the remote oceanic location of these areas makes them difficult to patrol both logistically and financially, and consequently they are under constant threat by illegal fisheries [5,6].

One such example is the Isla del Coco National Park (PNIC) (Costa Rica) in the Eastern Tropical Pacific Marine Corridor. It is an uninhabited island, located 550 km southwest of the Pacific coast of Costa Rica [7], reached only after a 36-hour boat ride from the mainland. Isla del Coco was declared a national park in 1978 but the marine portion was only included in 1984 (5 km around the island) [8]. Both in the terrestrial and marine area of the PNIC it is not allowed to exploit its natural resources [8]. The park was declared a UNESCO World Heritage site in 1997, and the MPA was extended in 1991 (to 15 Km around the island) and again in 2001(up to 12 nautical miles, 22.22 Km). The park has also been a Ramsar site since 1998 [9]. In 2011, a special management area was created around Isla del Coco National Park, the Seamounts Marine Management Area, which contains a marine protected area of 9,640 km^2 where the longlining is regulated and bottom trawling and purse seining are prohibited [9,10].

The PNIC is recognized as a sanctuary for migratory pelagic species such as yellowfin tuna (*Thunnus albacares*) and different sharks (Carcharhinidae, Alopiidae and Sphyrnidae), especially the silky shark (*Carcharhinus falciformis*) [11-13]. The wide prevalence and abundance of these pelagic species in the waters off the PNIC and its surrounding areas is the main reason for the numerous incursions of fishing vessels into the MPA, which is also one of the main species threats [6]. This illegal activity is encouraged by the increasingly high economic value of yellowfin tuna and sharks in both domestic and international markets [14,15] for both their meat and their sub-products: liver oil, skin and shark fins [16-22].

The illegal gain or benefit in a commercial fishery is the main reason that usually temps people to violate a fishery regulation [23-25]. The amount of potential illegal gains in fisheries often can be quite large. For example, in fishing in New England, it was found that a large percentage of fishers were making illegal earnings of around a quarter of a million dollars a year. According to Sutinen, et al. (1990) [26], in some cases, illegal fishing trips earned three times the revenue of legal trips.

The expected penalty should work to dissuade people from committing illegal fishing. However, in general, the penalties are not high compared to possible illegal earnings. For example, in the groundfish fishery of the Northeast United States [26], illegal fishers are estimated to have earned around $15,000 per fishing incursion, resulting in illegal earnings of $225,000 during 1987. Typical penalties this activity ranged from $3,000 to $15,000 [26].

The magnitude of the penalty or sanction is often constrained by law and determined by the judicial system [27]. The typical odds of being caught fishing illegally are below one percent [28, 29]. This pattern of low certainty and severity of sanctions relative to potential illegal gains tends to appear in most fisheries [30,31].

In PNIC, when illegal boats are detected in the area by patrol boats, fishers commonly cut their lines and, unless the Park rangers can intercept them, they are not arrested and do not suffer any sanctions [5]. However, when wardens do manage to intercept illegal boats, they can only give a written and/or verbal notification and fishers are processed only in case of recidivism of the crime. Even after the arrest, the probability to be convicted or to have severe sanctions is very limited given that prosecutions can be delayed by more than eight years [5].

Estimating the level of illegal fishing is, by its very nature, extremely difficult. Although there are several studies of the level of IUU (Illegal, Unreported and Unregulated) fishing and its relation to socio-economic indicators [32-37], and indices of governance (i.e. Government Effectiveness, Regulatory Quality, Rule of Law and Control of Corruption) [5,38], few studies have explored the biological and physical factors that influence the illegal fishing spatial distribution.

Potential and actual illegal gains are dynamic and are influenced by several conditions in the fishery, for example, prices and market conditions, judicial system, biological conditions (size, location and composition of the fishery resource), which are constantly in flux, influencing where and how fishers can earn the most income [26].

In particular, Arias et al. (2016) [5] analyzed the spatial and temporal distribution of illegal fishing in PNIC to optimize the effort patrol and constraints on the process arrest/citation, prosecution and conviction the illegal boat. In this study we updated this analysis, using in addition physical and biological covariables, and performing a cost-benefit analysis of illegal fishing to better identify the implications for management. In particular, we analyzed a database (2003-2010) of illegal fishing activity in the Isla del Coco MPA with multiple objectives, such as: (1) to understand the spatial-temporal patterns of this activity, (2) to identify other areas that could be prone to illegal fishing but are currently undetected, (3) to assess the more profitable areas, and its potential economic tradeoffs in relation to possible benefits and costs. Our results provide useful information, which can be used by managers to optimize enforcement in the studied area and to deter illegal fishing and thus increase the protection of pelagic species.

4.5. Material and methods

4.3.1. Data of illegal fishing operations

We analyzed a dataset covering 8 years (2003-2010) of illegal fishing records from PNIC (Fig. 1) that were compiled by Park rangers, the Coast Guard and *MarViva* [39] (an NGO that assisted with patrols). The dataset included information on 360 illegal fishing records observed from September 2003 to June 2010. For some months during the time series no information was available. The number of patrols was not constant during the time series due mainly to the oceanographic conditions, logistical difficulties and the financial expense (e.g. availability of boats, etc.).

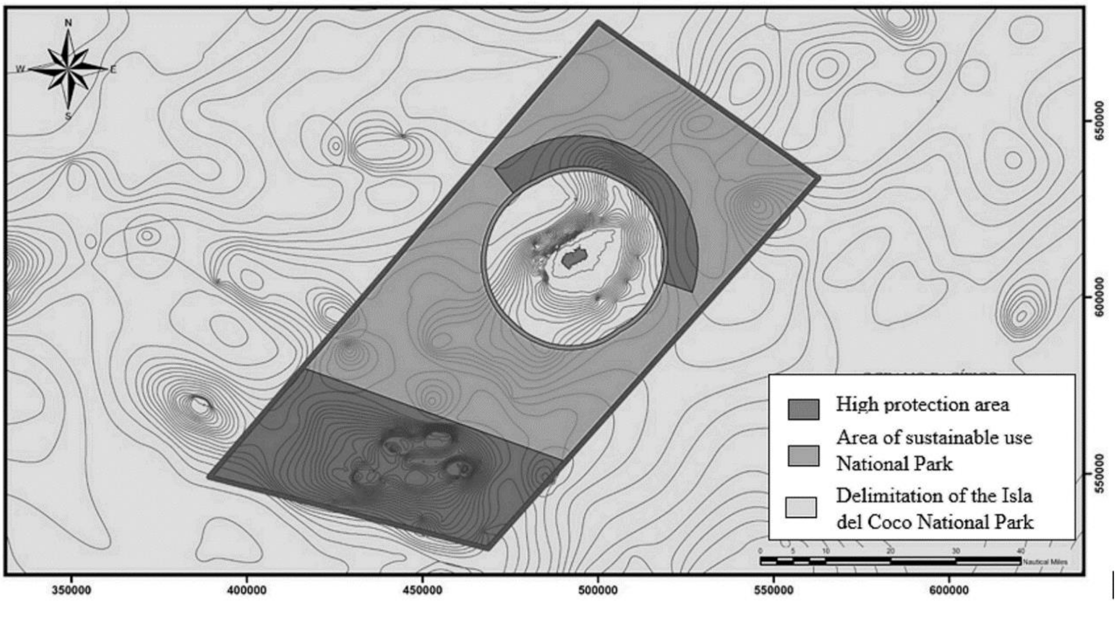


Fig. 1. Map of Isla del Coco National Park. (http://www.mpatlas.org/mpa/).

Additional information contained in the dataset was related to the geographical location (longitude and latitude) of the illegal fishing operations observed, the number of confiscated longlines and the number of individual yellow tuna and shark caught in each long line. It is worth mentioning that this dataset includes only illegal and unreported catches but exclude discards. Using the grid index features tool in ArcGIS (version 10.1) a grid of 0.03 x 0.03 degree cells was created for the studied area. Illegal fishing was quantified as the number of times that this activity was observed in a grid cell. Since we did not have patrol effort information, we were not able to estimate catch per unit effort.

4.3.2. Species and economic data

The main species caught by illegal fishing were yellowfin tuna and silky shark. In order to obtain an estimated abundance of these two species we used underwater visual census data of the Undersea Hunter Group [40], which is a private diving company that operates in Isla del Coco [41,42]. Species density maps by quarter of the year were generated the Radial basis functions (R, F) tool in ArcGIS with the same spatial resolution (0.03 x 0.03 degree) as the illegal fishing data (Fig. 4 and Fig.5). In order to compute the economic trade-offs of an illegal fishing operation in the Isla del Coco MPA we estimated the economic value of the caught species found by the patrollers, the costs of the fuel for a travel to the island and the value of the confiscated longlines. First, we extracted the ex-vessel prices of the two main caught species for Costa Rica’s Exclusive Economic Zone (EEZ) from the Sea Around Us website [43]. This database included reconstructed landings that combine official reports from the Food and Agriculture Organization of the United Nations (FAO) (https://www.fao.org) and reconstructed estimates of Illegal, unreported and unregulated (IUU) fisheries data [44,45]. Finally, we assigned a mean value of $2.32 USD to each kg of yellowfin tuna taking into account an average weight of 30.8 kg for each individual caught by illegal longlines. This average weight was considered taking into account the most frequent weight of individuals caught by longlines in the area [46-50].

Furthermore, we assigned a mean value of $100 USD for each kg of shark fin, bearing in mind that 1.25 sharks (of medium average size) are equivalent to one kilogram of fin. This information was provided by the "*Misión Tiburón*" NGO [51] that works specifically in the area for the conservation of sharks.

Regarding the cost of fuel, the vessels observed near the PNIC were usually commercial fishing vessels belonging to Costa Rica of medium and advanced scale whose main fishing gear is a line [52,53]. These illegal fishing boats can receive subsidized fuel, thus allowing them to reach the Park with a cost of $0.55 USD per liter of fuel [22].

In order to contrast these economic data, we conducted structured interviews with six key informants in the fishing sector with the purpose of corroborating that, the values of kg of shark fin and kg of yellowfin tuna obtained indirectly, agreed with the information provided by the sector. In addition, questions were also asked about the average price of the standard longline used by the illegal fishing boats. Based on these interviews a value of $150 USD was assigned to each confiscated longline. Finally, a review of the gray literature of Costa Rica was carried out to double-checking the obtained information.

4.3.3. Mapping illegal fishing distribution

Generalized Additive Models [54] were used for modeling illegal fishing distribution. A GAM is a regression-like model that uses smoothing splines to relate response and explanatory variables and thus allows non-linear and non-monotonic relationships [54]. Specifically, the number of illegal fishing records per grid cell was used as a response variable. As count data are often heavily tailed, we used an overdispersed Poisson distribution with a variance proportional to the mean, and with a logarithmic link function.

Expected number of illegal fishing in each grid cell was related to environmental, temporal and biological covariates. Specifically, the environmental variables we considered were depth (in meters), distance to coast (in meters), slope (in %) and rugosity of the seabed as potential descriptors of the seabed around Isla del Coco (see Supporting information, Appendix: Fig. A1). These bathymetric features, except rugosity, were derived from the MARSPEC database [55]. MARSPEC is a world ocean dataset, with a spatial resolution of 0.01 x 0.01 degrees, developed for marine spatial ecology [56]. Conversely, the rugosity of the seabed was derived from the depth map using the *terrain* function of the *raster* package [57] in the R software [58]. This function measures the rugosity as the variation in the three-dimensional orientation of the eight neighbor grid cells. Commonly, unconsolidated seabed, such as mud and sand, corresponds to low rugosity values, thus, high rugosity values are associated with potentially rocky substrate. All the environmental variables were aggregated at a spatial resolution of 0.03 x 0.03 for the illegal fishing data using the *raster* package of the R software.

Autocorrelation (ACF) and Partial Autocorrelation Function (PACF) were tested to verify the existence of annual and seasonal non-random temporal patterns in the dataset using the *stats* package of the R software. No correlation was found at year level while a non-random distribution of illegal fishing records was detected at seasonal scale. For this reason, the quarter of the year (which indicates the period when the illegal fishing was observed) was used as a temporal effect, in order to verify intra-annual variations on the illegal fishing distribution. The abundance (i.e. the number of individuals) of yellowfin tuna and silly shark by grid cell was used as a biological variable.

Before their use in GAMs, all the predictors were explored for collinearity, outliers, and missing data following the procedure of Zuur et al. (2010) [59]. Variables with a Pearson's correlation higher than 0.70 and with a VIF higher than 3 were alternated in the models (see Supporting information, Appendix: Fig.A2). GAMs were fitted in the R software using the *mgcv* package [60] in which degrees of freedom for each smooth function are determined internally in model fitting and thin plate regression splines are the default [61]. We limited the amount of smoothing to 4 degrees of freedom for each spline to avoid overfitting that would have no ecological meaning [62] and we implemented a cyclic cubic regression spline for the quarter variation. For the predictors in which we detected a linear relationship with the response variable, no smoothing spline was applied.

To account for the spatial autocorrelation in the data, we implemented the residuals autocovariate (RAC) approach [63] at both stages of the GAM model. Here the spatial autocorrelation was included by adding another term to the model (the autocovariate), which represents the influence of neighbor observations on the response variable at a particular location (1° square). For each model, the RAC approach was implemented as follows: first, the model selection was performed using a backward stepwise procedure based on four criteria, such as the lowest Unbiased Risk Estimator (UBRE) and Akaike information criterion (AIC) scores, the highest deviance explained (De %), and that all the predictors were significant. Second, residuals from the selected model were calculated for each grid cell and were used to compute the autocovariate by a focal calculation. This allowed cells from a selected neighbor to have a weight of 1 and all other cells a weight of 0. Finally, the residuals autocovariate was considered to be an explanatory variable in the previous model [63]. Spatial autocorrelation was tested for each model by calculating the Moran's index and carrying out a Moran statistical test (R package *spdep*, see [64]), which indicates a correlation between observations depending on the distance between them.

4.3.4. Computing the economic trade-offs of illegal fishing

In order to compute the economic trade-offs of an illegal fishing operation (P_{qi}) we computed fishing profitability, by quarter *q* and in a grid cell *i*, as the difference between expected benefits W_{bqi}, and total costs, W_{tqi}:

$$P_{qi} = W_{bqi} - W_{tqi}.$$

Expected benefits W_{bqi} from illegal fishing were computed in the conventional way [65]:

$$W_{bqi} = P_c * D_{cqi} * C_{cqi} * E,$$

where P_c is the average ex-vessel price per species group *c* (yellowfin tuna and silly shark), D_{cqi} is total density per species group *c* by quarter *q* in a grid cell *i*, C_{cqi} is the catchability coefficient (the probability of catching an individual yellowfin tuna or silky shark) by quarter *q* in a grid cell *i*, and *E* is the effort of illegal fishing by quarter *q* in a grid cell *i*. C_{cqi} was computed as

$$C_{cqi} = N_{ciq} / (L_{qi} * D_{cqi})$$

where N_{cqi} is the average number of yellowfin tunas and silky shark caught by illegal fishing by quarter *q* in a grid cell *i*, L_{qi} is the average number of confiscated longlines by quarter *q* and in a grid cell *i*, and D_{cqi} is the total density per species group *c* by quarter *q* in a grid cell *i*.

To calculate the effort E_{qi} of illegal fishing by quarter q in a grid cell i we used the predicted density obtained by RAC-GAMs. C_{cqi} and D_{cqi} of yellowfin tuna and silky shark individuals may be affected by migratory processes and consequently influence the benefits computation. However, given that species movements are unpredictable, no migratory component was incorporated into the model.

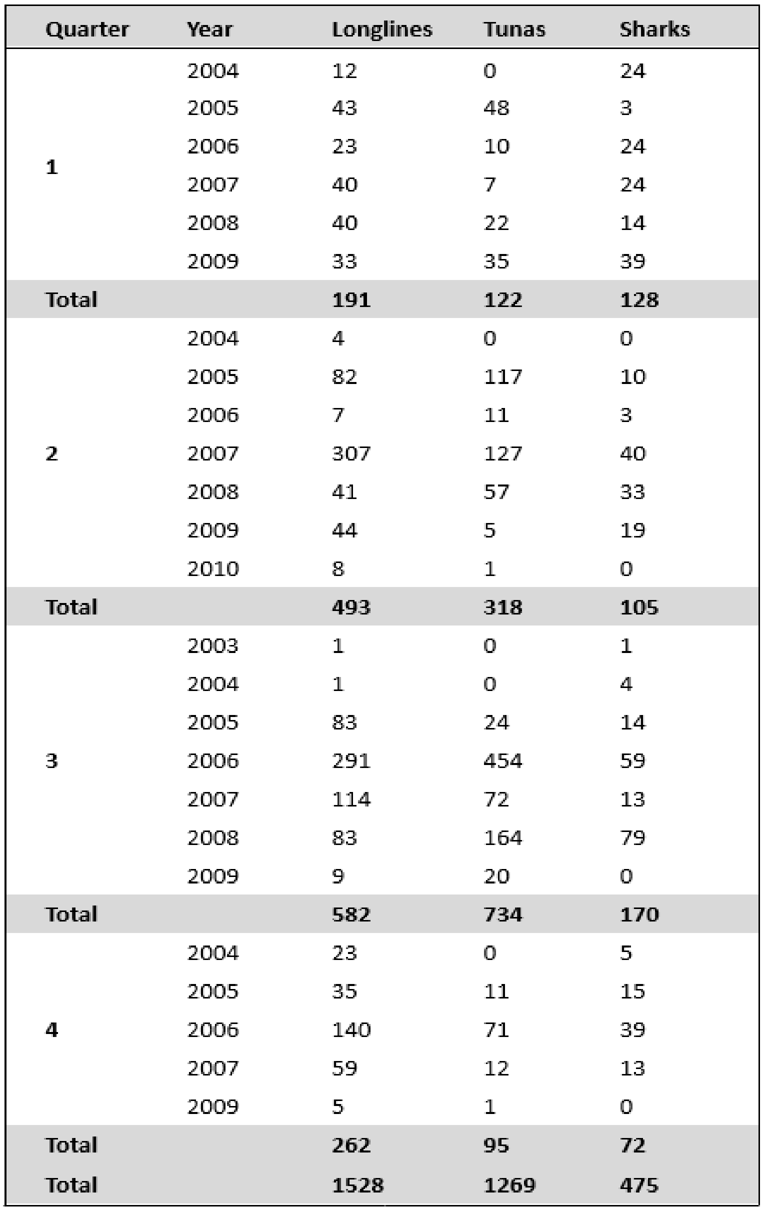
The total costs, W_{tqi}, by quarter q in a grid cell i were computed as the sum of the cost associated with traveling to a grid cell in terms of fuel, F_i, and the cost of a confiscated longline CL_{qi}. Specifically, CL_{qi} was computed by taking into account the average number of confiscated longlines by quarter q and grid cell i and the probability of detection p_i. As data on the patrol effort was not available, p_i was considered to depend on habitat structure and distance to the coast, which we hypothesized was greatest near the coast and particularly in waters surrounding seamount that are known to be a favorable habitat for aggregation of pelagic species [42].

4.6. Results

4.4.1. General results

During the 8 years of incursions in the Park, a total of 1528 longlines were requisitioned with a total of 1269 yellowfin tuna and 475 sharks (Table 1). The months with the highest number of longlines requisitioned were July-September (582) and April-June (493). During the months of July-September the highest number of yellowfin tuna (734) and sharks (170) were found. By contrast, during the fourth quarter, the smallest number of yellow tuna (95) and elasmobranchs (72) were found (Table 1).

Table 1. Numerical summary of the dataset. The variables are: the year in which the illegal fishing was recorded (2004-2009); the quarter- January-March (1), April-June (2), July-September (3) and October-December (4); the number of confiscated longlines; the number of yellowfin tuna and the number of sharks.

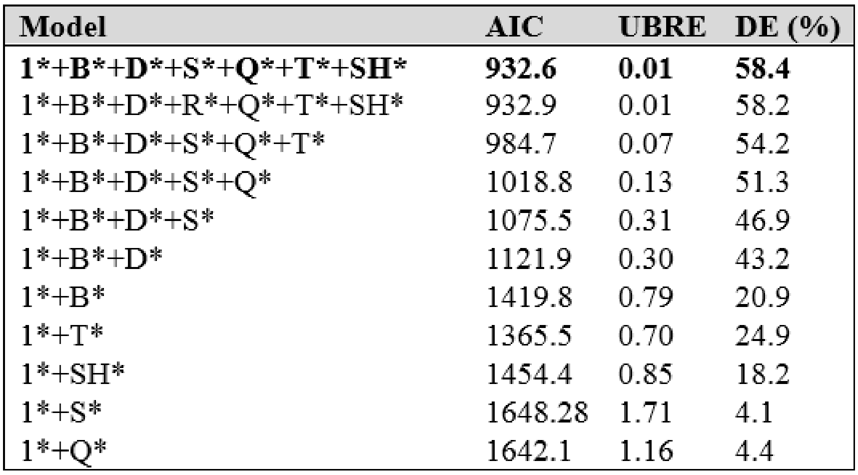


Quarter	Year	Longlines	Tunas	Sharks
1	2004	12	0	24
	2005	43	48	3
	2006	23	10	24
	2007	40	7	24
	2008	40	22	14
	2009	33	35	39
Total		**191**	**122**	**128**
2	2004	4	0	0
	2005	82	117	10
	2006	7	11	3
	2007	307	127	40
	2008	41	57	33
	2009	44	5	19
	2010	8	1	0
Total		**493**	**318**	**105**
3	2003	1	0	1
	2004	1	0	4
	2005	83	24	14
	2006	291	454	59
	2007	114	72	13
	2008	83	164	79
	2009	9	20	0
Total		**582**	**734**	**170**
4	2004	23	0	5
	2005	35	11	15
	2006	140	71	39
	2007	59	12	13
	2009	5	1	0
Total		**262**	**95**	**72**
Total		**1528**	**1269**	**475**

4.4.2. Spatial and temporal density distribution of illegal fishing

According to the GAM with the best fit (based on the lower AIC, UBRE, highest explained deviance and all significant variables), the illegal fishing distribution was mainly explained by the quarter of the year, bathymetry, slope of the seabed, distance to coast, and silky shark and yellowfin tuna abundance (Table 2). The explained deviance of the selected GAM was 58.4% and increased to 72.2% when the autocovariate residual spatial effect was included as an explanatory variable. This means that, taking into account the intrinsic spatial variability of the data, the deviance explained by the model increases markedly. This spatial variability is not explained by the other covariates, a signal that there are other spatially structured processes not included in the model that are important to explain the distribution of illegal fishing.

Table 2. Comparison of the most relevant GAM models performed to understand the illegal fishing abundance and distribution. Selection of the model was based on the scores of the Akaike information criterion (AIC), the Un-biased Risk Estimator (UBRE) and the total percentage of deviance explained by each model (% DE). Variable acronyms are: bathymetry (B), distance from the coast (D), slope (S), rugosity (R); Quarter (Q), abundance of the shark (SH), and abundance of yellowfin tuna (T). The best model is highlighted in bold. The significance of the predictors is indicated by *.



Model	AIC	UBRE	DE (%)
1*+B*+D*+S*+Q*+T*+SH*	**932.6**	**0.01**	**58.4**
1*+B*+D*+R*+Q*+T*+SH*	932.9	0.01	58.2
1*+B*+D*+S*+Q*+T*	984.7	0.07	54.2
1*+B*+D*+S*+Q*	1018.8	0.13	51.3
1*+B*+D*+S*	1075.5	0.31	46.9
1*+B*+D*	1121.9	0.30	43.2
1*+B*	1419.8	0.79	20.9
1*+T*	1365.5	0.70	24.9
1*+SH*	1454.4	0.85	18.2
1*+S*	1648.28	1.71	4.1
1*+Q*	1642.1	1.16	4.4

The spatial maps highlight that the areas with the highest concentration of illegal fishing operations are concentrated in shallowest waters with substrata with high slopes (Fig. 2), in the northeast of the Park where there is a seamount at 15 km from the island (Figs. 2, 3). Additionally, illegal fishing is preferably focused on the area with a higher abundance of yellowfin tuna and silky shark.

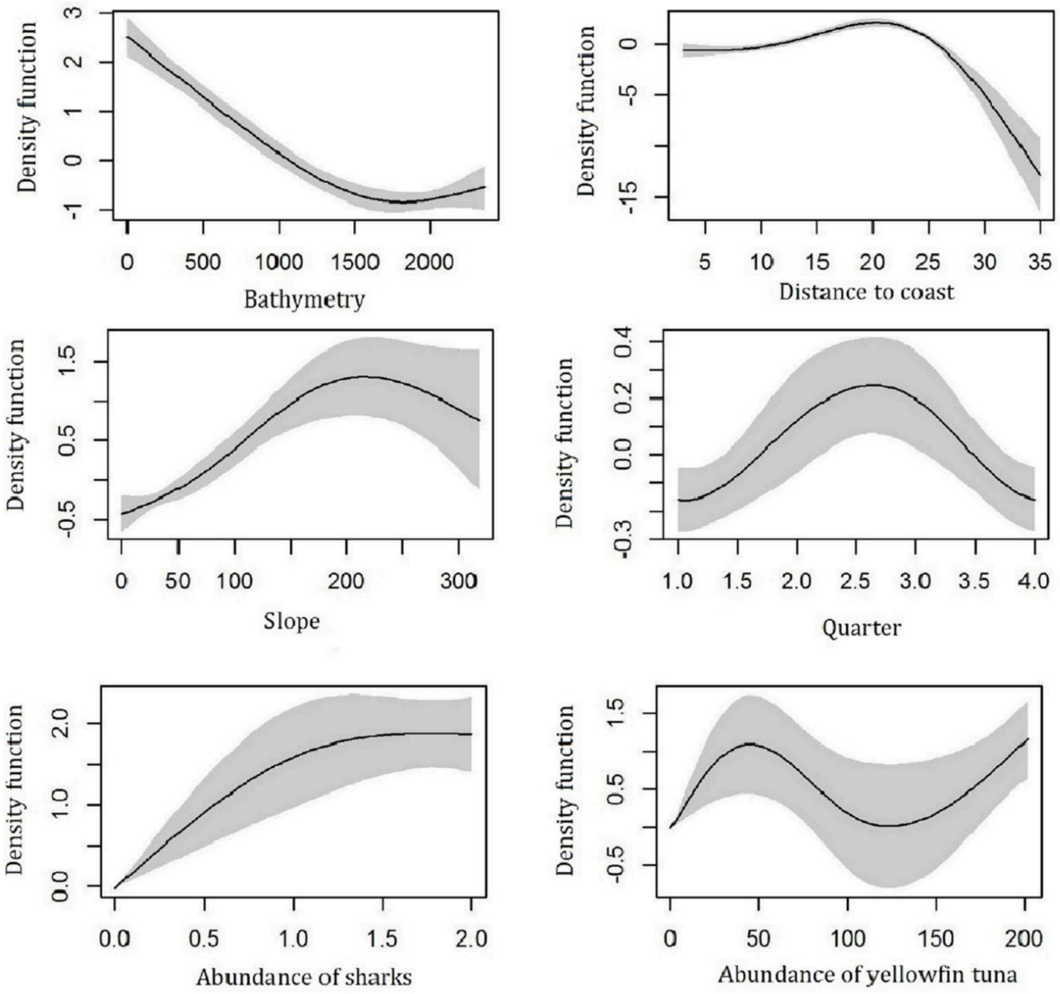


Fig. 2. Smooth functions for the selected covariates of the illegal fishing model. The solid line in each plot is the estimated smooth function, and the dashed lines represent approximate 95% confidence intervals.

The spatial-temporal maps suggest that the highest number of illegal fishing operations were between the second (July-September) and third (July-September) quarters, whereas the first quarter (January-March) recorded the lowest number of incursions (Figs. 2, 3b, 3c).

The Moran spatial autocorrelation test was significant (Moran’s index 0.06 < 2.2e16), showing an absence of spatial autocorrelation and that therefore the RAC method worked correctly.

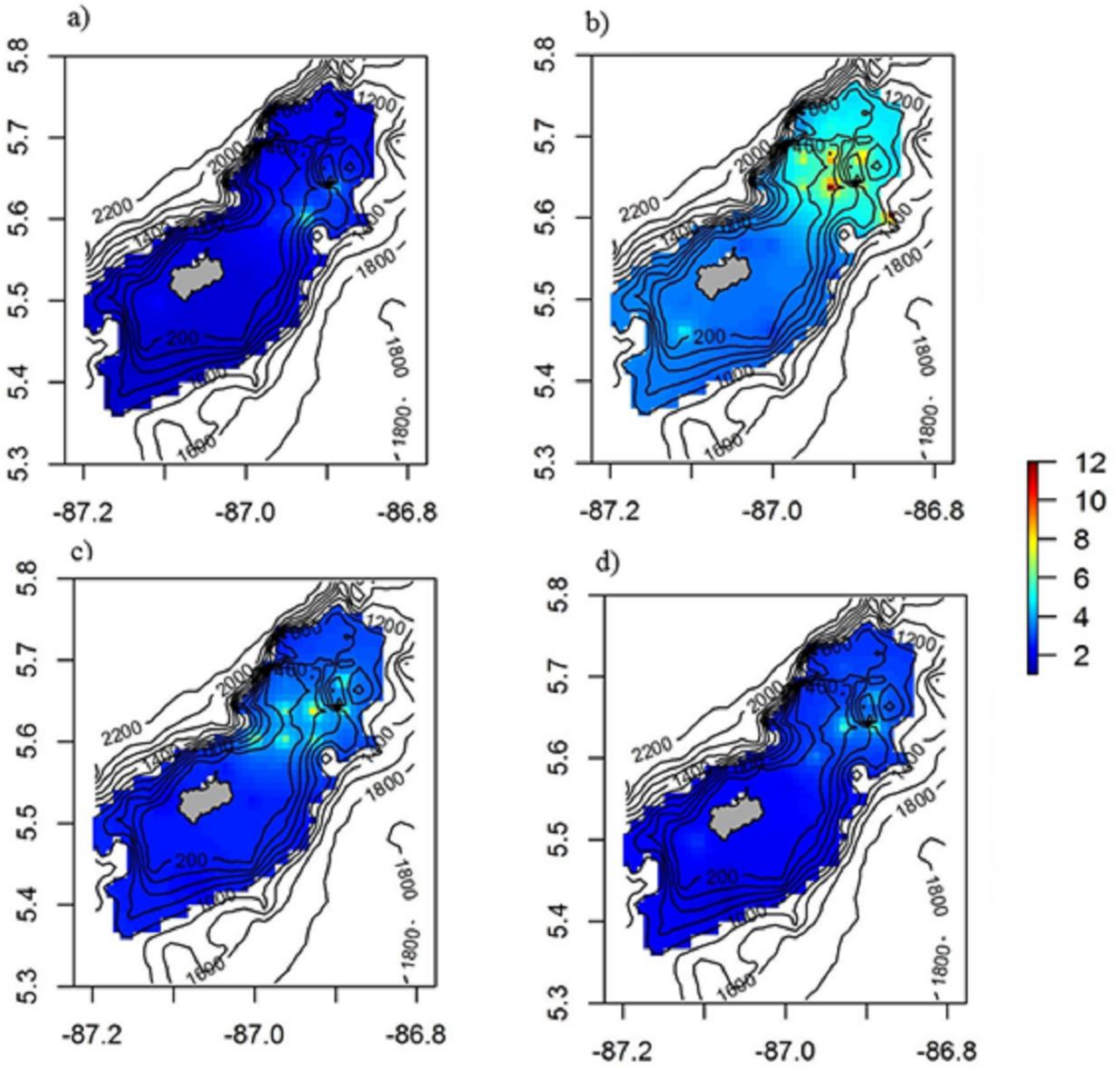


Fig. 3. Spatial distribution maps of illegal fishing operations in PNIC aggregated at quarterly intervals: January-March; b) April-June; c) July-September; d) October-December.

The highest density of yellowfin was observed in the fourth quarter (October-December), with a spatial expansion throughout the national park area although its highest concentration was in waters surrounding the seamount (Fig. 4d). Instead, the silky shark recorded its highest concentration between April and June (Fig. 5b) in the waters surrounding the seamount and a high density in shallow waters near Isla de Coco in the first (January-March) (Fig. 5a) and the fourth (October-December) quarter of the year (Fig. 5c)

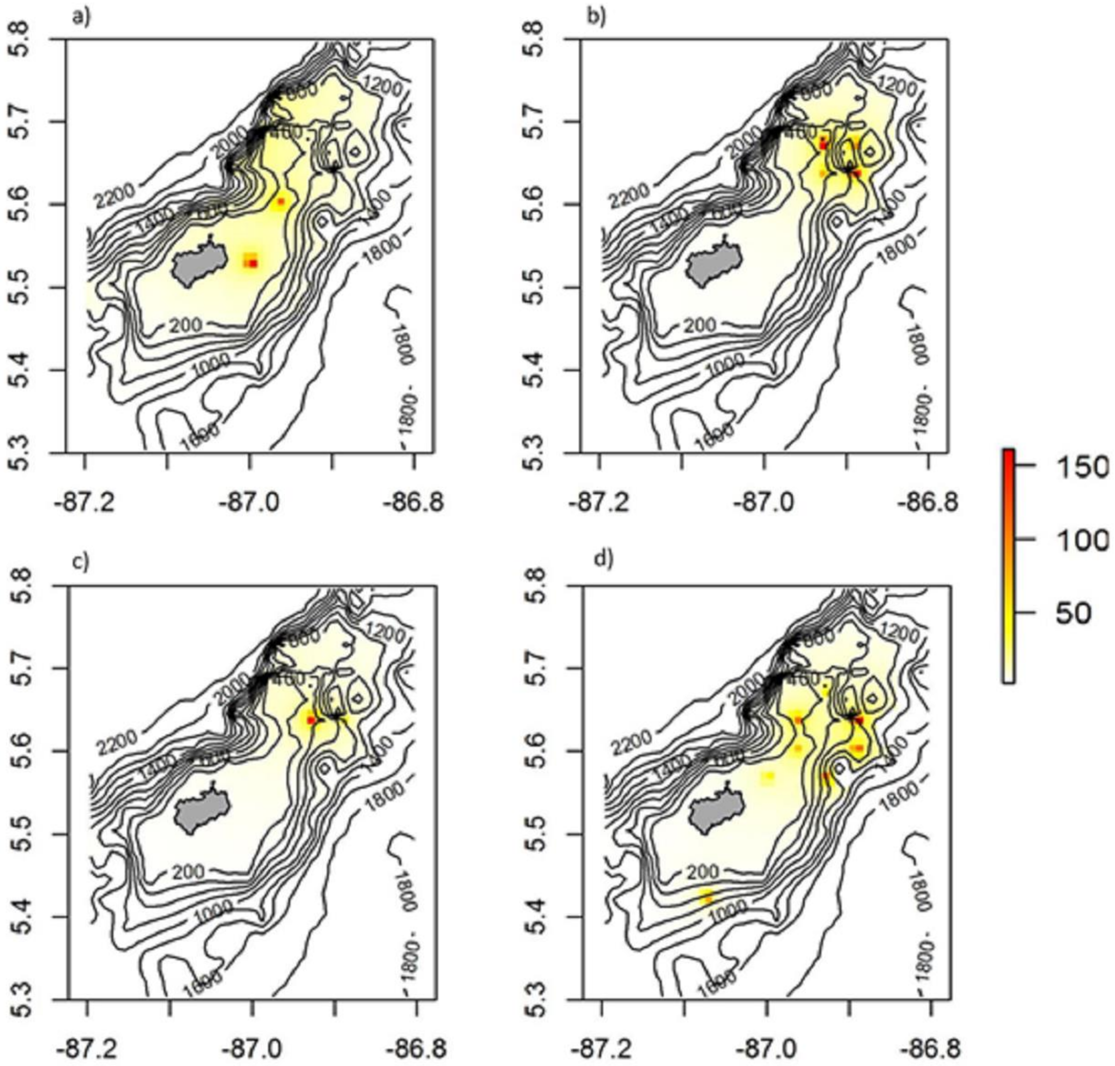


Fig. 4. The spatial patterns of the yellowfin tuna abundance (n. of individuals) in PNIC aggregated in at quarterly intervals: a) January-March; b) April-June; c) July-September; d) October-December.

Density maps of silky sharks and yellowfin tuna (Figs. 4, 5) are an indicator of other areas that could be prone to illegal fishing but are not currently detected. In the third quarter, the density of yellowfin tuna, silky shark and the density of illegal fishing are high in the seamount area (Figs. 3c, 4c, 5c). In the first quarter of the year the density of yellowfin tuna (Fig. 4a) and silky shark (Fig. 5a) is higher near Isla de Coco but illegal fishing is almost non-existent in this area (Fig. 3a). Similarly, in the months of October-December, the density of yellowfin tuna and silky shark (Figs. 4d, 5d) expands in waters distant from seamount, but instead, illegal fishing activity remains concentrated on the seamounts (Fig. 3d).

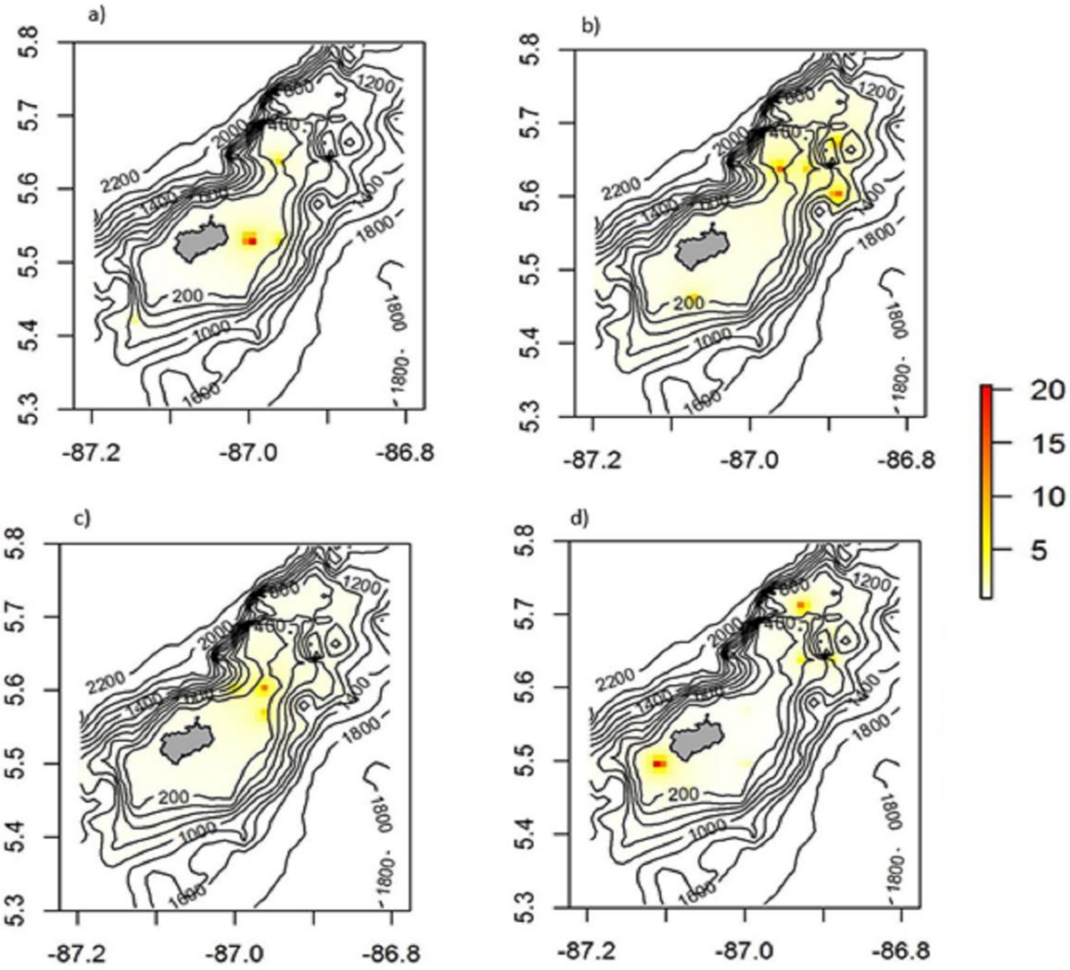


Fig. 5. The spatial patterns of the silky shark abundance (n. of individuals) in PNIC aggregated in at quarterly intervals: a) January-March; b) April-June; c) July-September; d) October-December.

4.4.3. The economic trade-offs of illegal fishing

Overall, the highest expected benefits as highest expected costs occurred in the northeast of the Park in waters surrounding a seamount (Figs 6,7) where there are high concentrations of pelagic species and the probability of detection was the highest. The second and third quarters had the highest expected benefits (Fig. 6b, c) and the highest expected costs (Fig. 7b, c), whereas the first quarter had the worst.

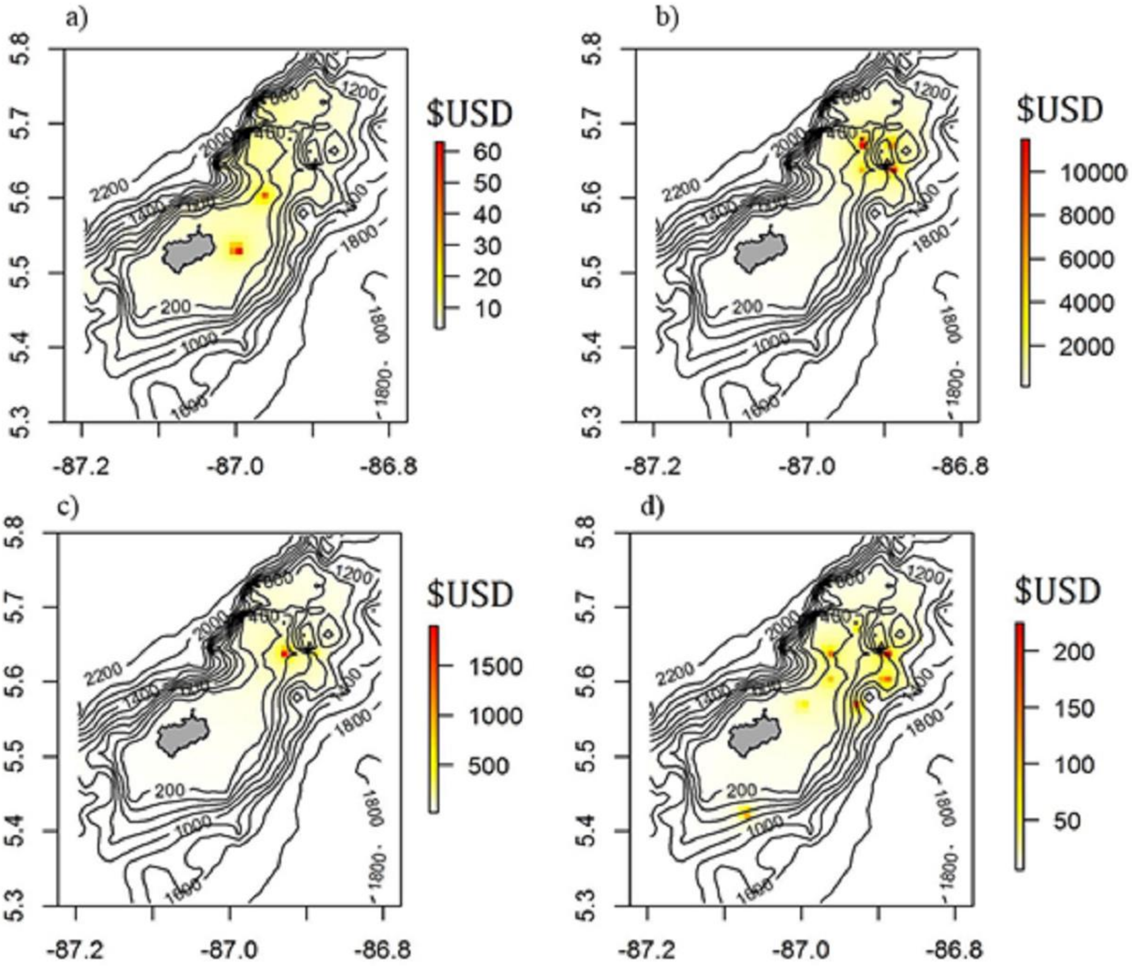


Fig. 6. Spatial distribution maps of the benefits ($USD) of illegal fishing in PNIC aggregated at quarterly intervals: a) January-March; b) April-June; c) July-September; d) October-December

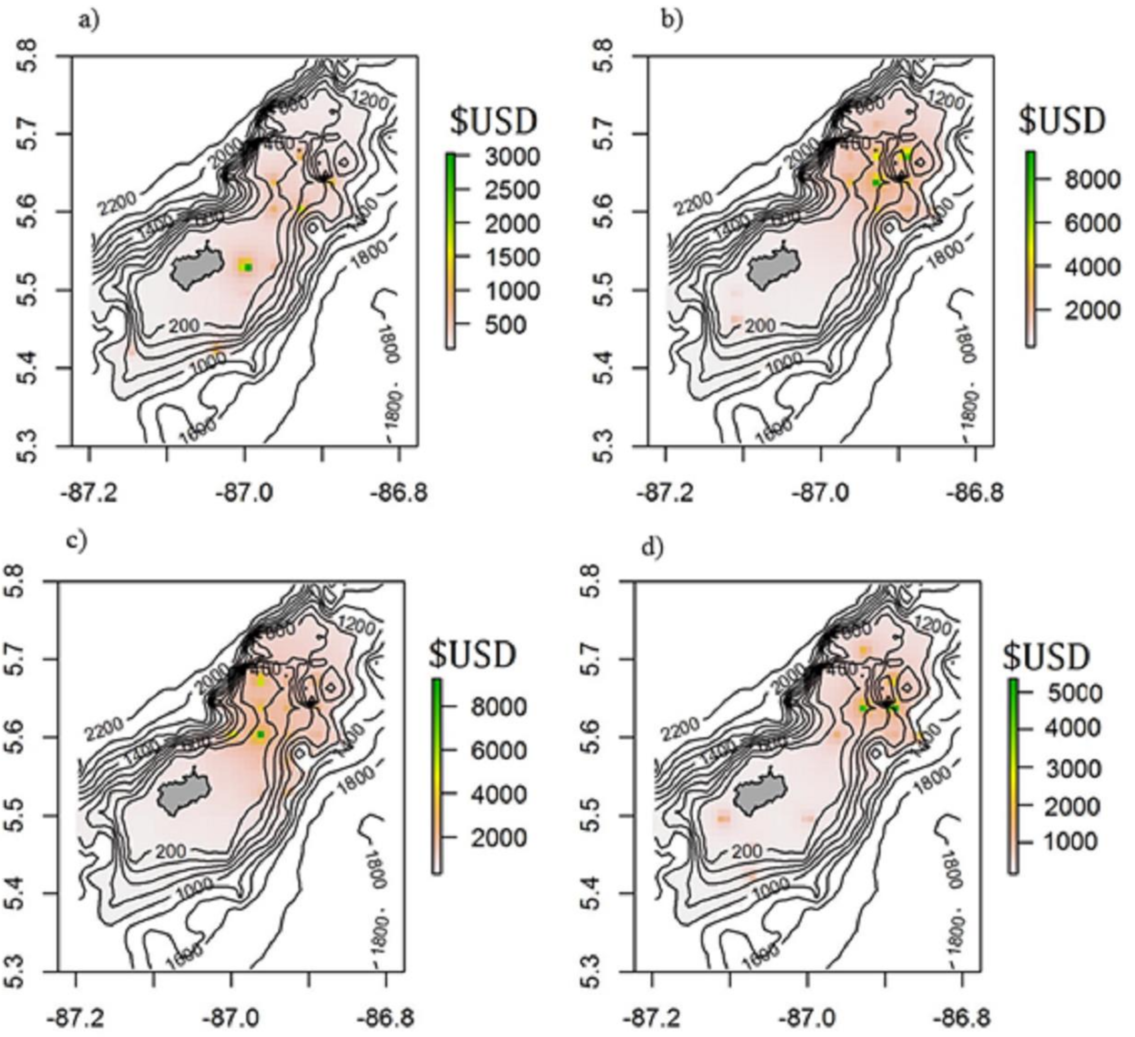


Fig. 7. Spatial distribution maps of the costs ($USD) of illegal fishing in PNIC aggregated at quarterly intervals: a) January-March; b) April-June; c) July-September; d) October-December

The spatial trend of profitability highlighted that the second quarter of the year is the period in which the excepted profits will be highest, particularly in the waters surrounding the seamount (Fig. 8b).

All the results suggest that the highest risk area in PNIC is in the waters surrounding the seamount, and this risk is highest between April and September.

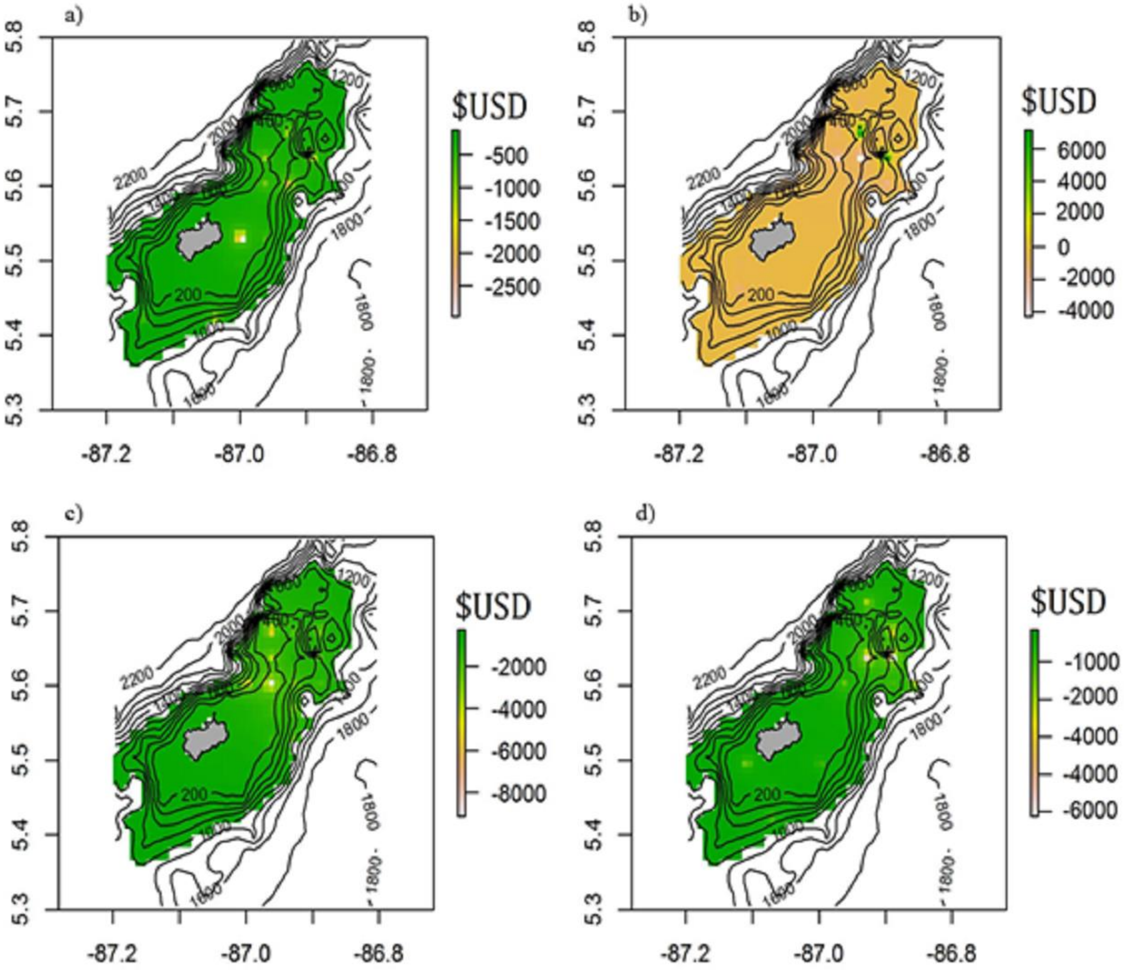


Fig. 8. Spatial distribution maps of the profits ($USD) of illegal fishing in PNIC aggregated at quarterly intervals: a) January-March; b) April-June; c) July-September; d) October-December.

4.5. Discussion

There is an urgent need to quantify the impacts of illegal fishing and define management practices that allow for the recovery and conservation of exploited stocks. The extent of illegal fishing is particularly critical as a driver of overexploitation of marine resources. However, the lack of data at proper spatial and temporal scales limits the evaluation of illegal fishing and effectiveness of management practices.

In this study, we provided new insights about illegal fishing in the Isla del Coco National Park. In particular, we assessed the spatial-temporal distribution of illegal fishing over an 8-year period in order to estimate the influence of environmental, biological and temporal factors on this activity, to identify other areas that could be prone to illegal fishing but are currently undetected, as well as the more profitable areas and the economic tradeoffs of this activity.

Results obtained on the distribution of illegal fishing, as well as the findings obtained by Arias et al. (2016) [5], indicate that the highest concentration of this activity is around the seamount area. Previous studies have observed that illegal fishing is most present where monitoring is more difficult, for example in the most remote areas of the island [66], which was confirmed here by our predictive maps that estimated more frequent events of illegal fishing at further distances from the coast (around 15 km from the island, next to a seamount) and less frequent events in areas closer to the coast.

Moreover, the main factors that affect the distribution of illegal fishing were seabed bathymetry, slope, and abundance of yellowfin tuna and silky sharks. Isla del Coco sits atop the Coco Volcanic Cordillera, a submarine mountain off the southern coast of Costa Rica [13, 67], which apparently attracts pelagic species such as yellowfin tuna [68-71] and elasmobranch [72,73]. In fact, seamounts can increase the density of prey for these species [74-76] and thereby generate important aggregation sites for highly migratory pelagic species [76]. On the PNIC seamount [77] specifically a high concentration of yellowfin tuna and other pelagic fish have been observed [35].

Temporal trends found in this study indicate a higher frequency of illegal fisheries and target species in the second and third quarters of the year as has been observed in other studies in the same area. For example, Castro et al. (2008) [78] reported a higher number of illegal fishing between June and December and Villalobos-Rojas et al. (2014) [79] observed a higher density of yellowfin tuna between May and June.

This suggests an increase in illegal fishing during the rainy months (May-October) in the studied area. This could be to the fact that rainy months have a higher concentration of nutrients, thus causing an increase in the biomass of predators, such as tunas and sharks [6,49]. In this context, Arias et al., (2016) [5], found that the third quarter of the year had the most incursions in this area, favoured not only by the oceanographic conditions but also by the lunar cycle. This difference in results could be due to the different explanatory variables taken into account in the analysis and to the different database analysed. We analysed illegal fishing data in the period 2003-2010 with topographic, biological and temporal variables and Arias et al. (2016) [5] study 5-year dataset (December 2005-September 2010) and use bathymetry, months and lunar phases as explanatory variable.

The first (January-March) and fourth (October-December) quarters showed the lowest number of illegal fishing operations. This may be because illegal fishers change their target species, for example to the "*Dorado*" (*Coryphaena hippurus*) (Linnaeus, 1758), [6,79] and move their activities to other areas.

Overall the economic analysis suggests that illegal activity is particularly related to the high value catches and the potential gains from illegal fishing outweigh the potential costs of being caught. Indeed, the profitability of this activity is very high due to (a) the low probability of detection; and (b) the absence of economic sanctions or arrest in case of interception. These results show that exogenously imposing mild law does not achieve compliance but, on the contrary, encourages this illegal activity. If fishers are not intercepted, the cost that they have to pay is relatively easy to support, especially because fishing boats receive subsidized fuel, thereby allowing them to reach the Park [22]. These findings are in lines with others studies at local and global level that also concluded that the economic gains from illegal fishing are significant enough to motivate fishers to engage in this activity [5,80-83]. In this context, Sumalia et al. (2006) [33], in a study of the illegal fishing issue at global level, pointed out that, for an assumed 1 in 5 chance of being apprehended, fines for the vessels apprehended will have to be increased by 24 times for the expected cost to be at least as much as the expected benefits. In the Isla del Coco context this will imply a fine of almost $ 96 if the minimum sanction were applied and $ 1,152 if the maximum sanction were applied in the case of crime for illegal fishing of sharks [85] according to the base salary of 2019 [84,85] and the increase calculated by Sumalia et al. (2006) [33].

The expected profits from illegal fishing in the PNIC are mainly from April to June when aggregation of pelagic species is highest. The northeastern part of the Park, in waters that surrounding a seamount, is the area with most at risk of illegal fishing and should be intensively monitored. In any case, it may be more interesting to increase the probability of detection than to increase the fines. In this sense, density maps of silky sharks and yellowfin tuna show other areas that could be prone to illegal fishing at different periods of the year, but that are currently not detected as risk areas and not monitored. Knowing the spatial-temporal distribution of the main target species of illegal fishing throughout the year can provide a potential indicator of areas that, in the future, could be frequented by illegal fishers. This information is useful for planning the surveillance of the Coco National Park, but more importantly this approach could be extended to other protected areas.

In recent years foreign ships fishing illegally inside the PNIC area have been documented using data from Global Fishing Watch, a satellite-monitoring platform. FAICO (Fundación Amigos de la Isla del Coco), a Costa Rican non-profit organization dedicated to supporting the protection of Cocos, is working with the Costa Rican government, including the Ministry of Environment and Coast Guard, to help strengthen policies to combat illegal, unreported and unregulated (IUU) fishing. Policymakers have integrated the FAICO report into a new and recently approved monitoring, control and surveillance plan for the Cocos and the surrounding EEZ.

However, other policies could also be adopted in addition to enforcement in PNIC and particularly at-risk areas. Indeed, ports closer to these risk areas are more vulnerable to illegal fishing than those farther away [80]. Applying pressure to these ports of convenience to tighten up their procedures for monitoring vessels and their catches could decrease the risks of illegal fishing. Moreover, longlines should be more closely monitored through stringent licensing regulations as they comprise the largest group of all vessels blacklisted by both Greenpeace and Regional Fisheries Management Organizations [81].

This study showed that the species that are caught illegally in large quantities are those that are abundant in the area, such as yellowfin tuna and sharks, and are accessible to the fishing fleets of many countries. The fight against illegal fishing should increase and include market control. Catch certification programs are among the most important and commercially significant measures that some regional fisheries management organizations could apply [82,83]. Their main value lies in the fact that they ensure the traceability of fish and fish products that reach the markets and certify that the capture has been carried out in accordance with national, regional and international conservation and management measures. In this way, catches from illegal fishing would not have access to markets. At the same time, they provide data on catches, on the amount of fish traded and, on the countries, involved in that trade. With this information, regional fisheries management organizations can make more effective decisions about the management and compliance of their conservation measures [86,87]. Anticipating sites potentially visited by illegal fishermen in the future and efficiently organizing patrols can be the basis for optimizing surveillance in PNIC and in general, in other marine protected areas. To adapt to each specific case, it is necessary to know the continuous records of the patrols present in the study area and to create geo-referenced distribution maps that provide the necessary information. The presented results presented could be improved if information on patrol effort were recorded and provided. In particular, GPS tracks of the patrol, or at areas monitored/time spent patrolling versus attending to infractions.

4.6. Conclusions

Conservation and sustainable use of high seas resources is becoming increasingly important due to the increasing trend of irregular exploitation. National, regional and international efforts must work together to ensure an application of surveillance, traceability and sanctions that ensures a sustainable exploitation of offshore resources. Tools such as temporal spatial distribution maps applied to illegal fishing activity, density of target species and benefits - costs of illegal fishing, can help to make appropriate decisions with conservation. With sustainable exploitation, the international community could benefit substantially by ensuring a future without loss of marine diversity on the high seas and protecting market values for the benefit of today and future generations.

4.7. Supplementary Material

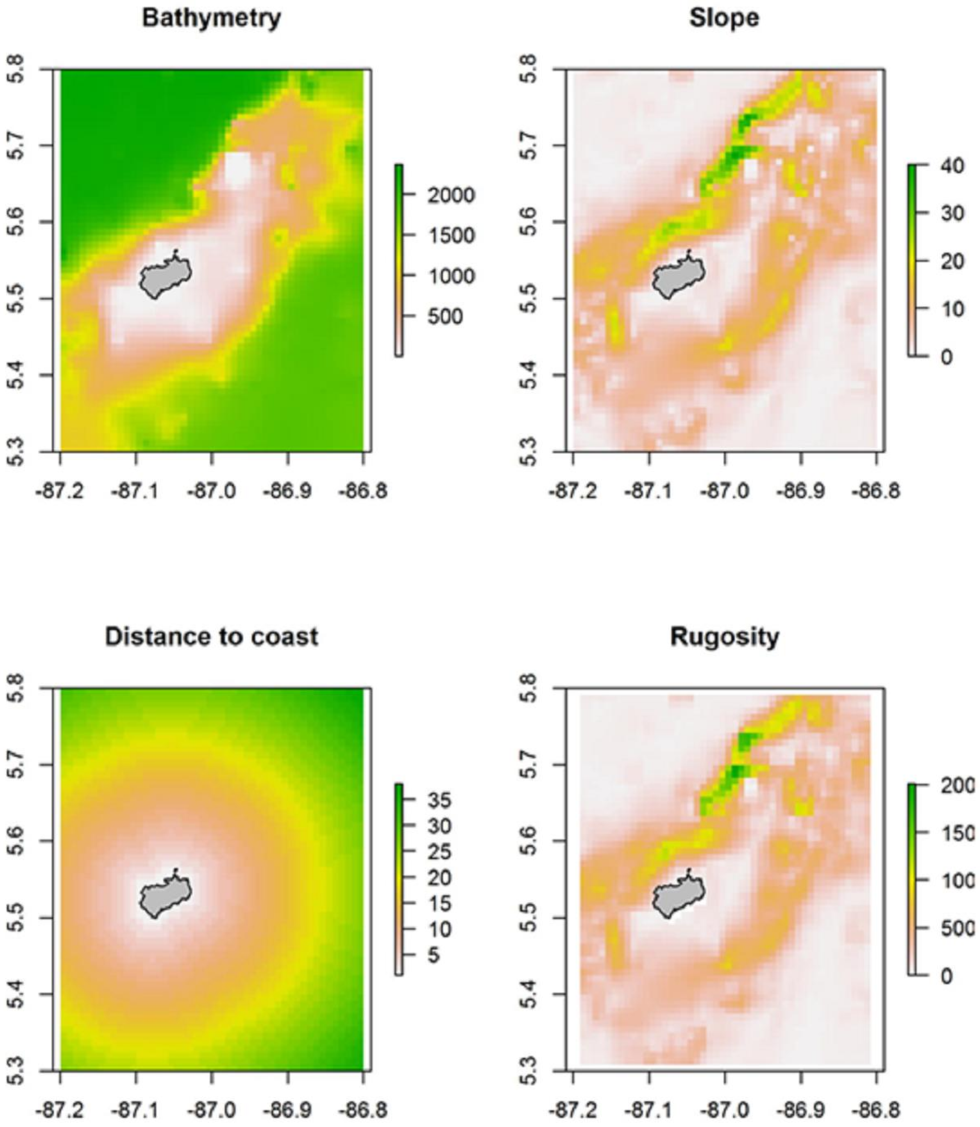


Fig. A1. Supplementary Material. The spatial patterns of the environmental variables considered to be potential predictors of illegal fishing in the Isla del Coco National Park.

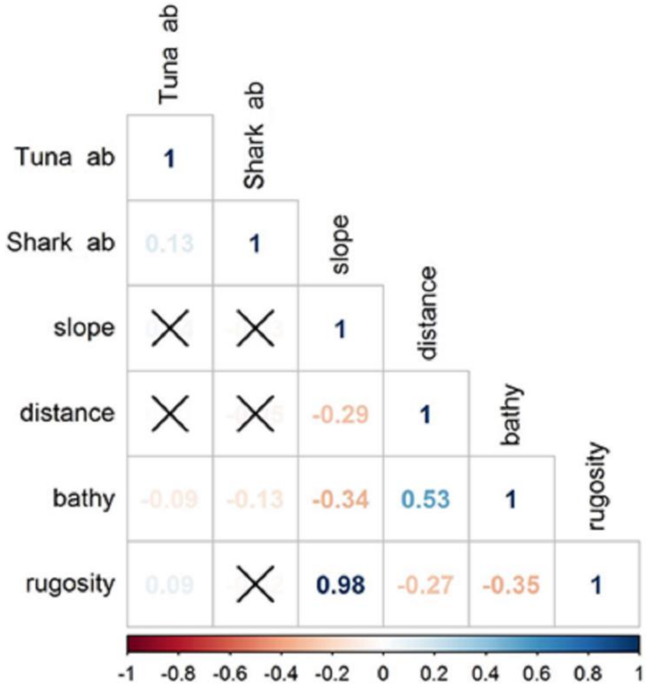
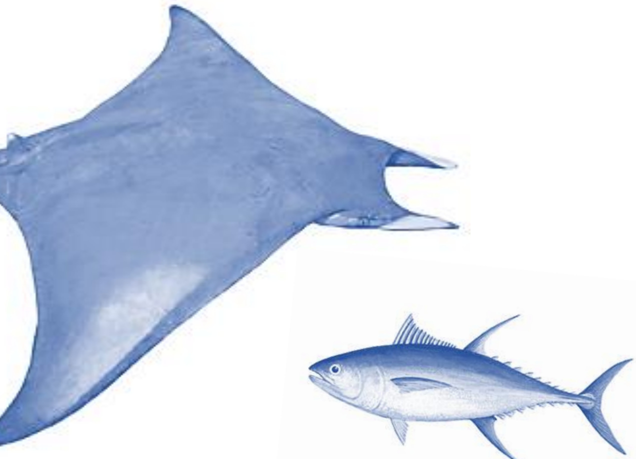


Fig. A2. Supplementary Material. Pearson's correlation matrix of explicative variables used in models.

Chapter 5:

General Discussion and conclusions



5.1. General discussion

Protecting pelagic ecosystems will be critical to meet global marine conservation targets, such as the ones of the Convention on Biological Diversity which calls to protect 10% of the worlds' oceans through marine protected areas (MPAs) by 2020 (Convention on Biological Diversity 2010). To meet these targets, there has been an increasing trend in recent years to create large-scale, mostly pelagic marine protected areas (PMPAs) [1]. These PMPAs may be large enough to guard against threats and incorporate key portions of far-ranging or migratory animal habitats and movements [2-5].

Many PMPAs, however, have only recently been designated or are in development stages, and very few have been in existence long enough to draw lessons relevant for the management of PMPAs elsewhere. Despite the sharp increase in the number PMPAs, little literature exists regarding on-the ground approaches to their management, in large part due to the relative newness of many largescale PMPAs.

Thus, the principal management challenges of PMPAs, are objectives, monitoring and compliance [6]. The dynamic nature of pelagic environments presents unique challenges for management. Enforcement of PMPAs can be particularly challenging because of the large and often remote areas to be monitored and the cost of reaching these areas [7]. Moreover, should be considered the cost-effectiveness, conflicting mandates, multi-agency coordination, and threats beyond PMPA boundaries.

Though PMPA objectives may vary, maintenance of the ecological system and protection of vulnerable species are common priorities. Establishing biological priorities for monitoring and enforcement means determining where the most vulnerable species or habitats are likely to be found and when they are most vulnerable [8].

Biological prioritization is built from baseline data of key species and habitats, as well as human uses and impacts. However, integrating key species, habitat and human use data (for example illegal fishing) will determine where the regions of highest threat and ecological significance co-occur [9-11]. In this step it is particularly important to consider where these areas occur temporally, as well as spatially.

To achieve these objectives, habitat models and predictive maps, such as those generated by the approach presented in this thesis, could be a useful source of information in the selection of areas for improved regional management or technical measure adoption. We believe that the use of this approach for constructing maps of the spatial distribution of vulnerable species may help the design of integrated programs for the more efficient management and control of marine resources.

In particular, two types of datasets were used in this thesis, underwater observations and illegal fishing data obtained by park rangers. Data from underwater observations collected by dive centers may represent one of the most important, but often underestimated, data sources for studying marine resources in places where fishing is prohibited. Data from underwater observations were used to improve our understanding of habitat utilization by elasmobranchs and yellowfin tuna in Isla del Coco National Park (PNIC).

Overall our results helped to evaluate the influence of the environment on the yellowfin tuna and on the majority of the species that constitute the elasmobranch community of the island. Additionally, the preferential habitats of these species were identified.

Illegal fishing data helped to understand the spatio-temporal distribution of this activity and to obtain predictive important results such as to detect other areas that may be prone to illegal fishing but are currently not detected. These identified possible locations of illegal fishing activity should be closely monitored. In addition, the economic trade-off of this illegal activity in relation to potential gains and the costs was evaluated in the fourth chapter. It is estimated that this illegal activity will continue over time because the potential benefits outweigh the potential costs of being captured. Higher taxes should be imposed to discourage this activity.

Overall, it should be noted that in our study the environmental and species data were sampled for a limited period of time and space, and thus fitted models can only reflect a snapshot of the expected relationship between the environment and the analysed species. Future studies should compare the spatial distribution of these species with a longer time series and using other sources of data. However, the results of this thesis could serve to promote a greater effort in data collection in the identified areas on which future research attempts should focus. For these reasons, similar studies on the distribution of elasmobranchs and other vulnerable species that cover other times of the year (seasons) are necessary to support conservation plans in this area.

5.2. Conclusions

With the available data, the main predictors of elasmobranch habitats in the PNIC were distance to shore, slope, and chlorophyll-a, indicating that elasmobranchs prefer shallow waters near the island and with different degrees of the seabed slope

Yellowfin tuna showed a tendency to decrease in abundance in the sampled period. Highest abundances were found in shallow and warm waters, with a high concentration of chlorophyll-a, and in the surrounding seamounts influenced by the topography and structure of the seabed.

Regarding the illegal fishing of elasmobranchs and yellowfin tuna, the main factors that influence the distribution of illegal fishing were the bathymetry of the seabed, the slope and abundance of yellowfin tuna and sharks. Predictive maps suggest an important trend in the abundance of illegal fishing between the second and third quarters of the year in the waters surrounding a seamount within the Park. Maps of the most profitable areas highlighted a specific risk location that needs to be closely monitored. In general, the potential benefits of this activity outweigh the potential costs of being captured and thus it is estimated that this illegal activity will continue over time.

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Resumen

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Chapter 2: Abundance and distribution patterns of *Thunnus albacares* in Isla del Coco National Park through predictive habitat suitability models

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Chapter 4: Illegal fishing in Isla del Coco National Park: spatial-temporal distribution and the economic trade-offs

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Chapter 5: General discussion and conclusions

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